

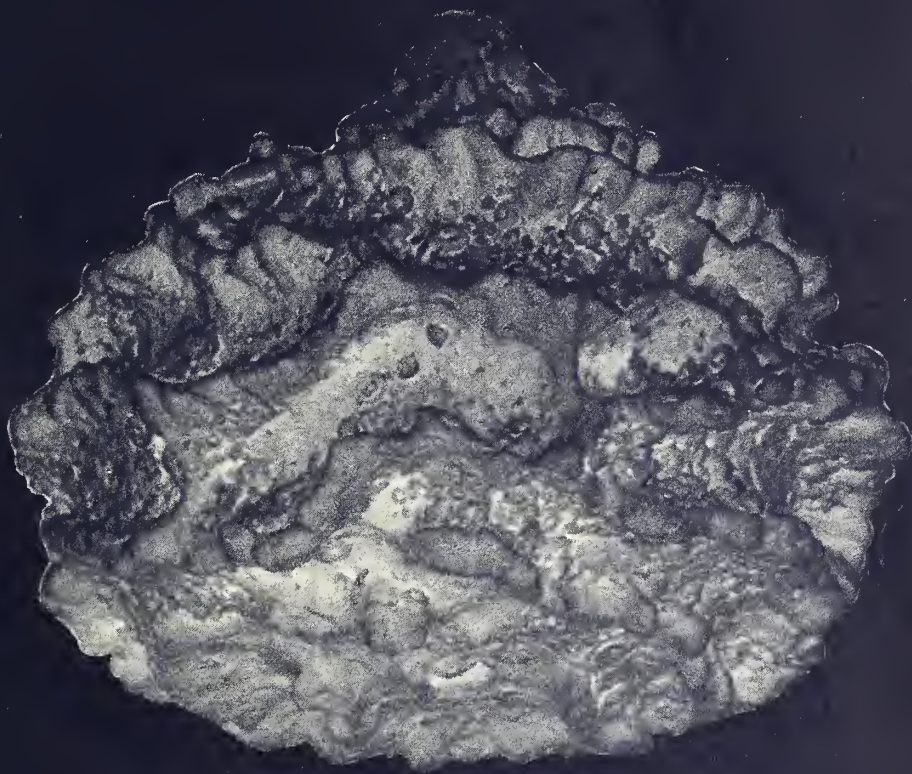




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Cover: *Bolboforma intermedia* Daniels and Spiegler (Incertae Sedis, possibly a calcified algal cyst) from Site 552A, southwest margin of Rockall Plateau, late Miocene NN9-10. $\times 800$. *Bolboforma* was planktonic and cysts are found in epicontinental shelf sea deposits, thus providing a useful biostratigraphic link with oceanic sequences.

THE UPPER JURASSIC DIAPSID *LISBOASAUROS* *ESTESI*—A MANIRAPTORAN THEROPOD

by ANDREW R. MILNER and SUSAN E. EVANS

ABSTRACT. *Lisboasaurus estesi* from the Upper Jurassic of Guimarota, Portugal was first described as an anguimorph lizard. Reexamination of the holotype and referred specimens has revealed the presence of thecodont teeth and an antorbital fossa, leading to the conclusion that *L. estesi* represents a small archosaur and not a lizard. Features of the dentition including labio-lingually compressed crowns with unserrated carinae, waisting between the root and the crown, and expanded roots, suggest that *L. estesi* belonged within the troodontid dinosaur–bird clade and, less certainly, within the Avialae (*Archaeopteryx* plus all later birds). It may thus be the earliest avialan. A second species in the genus, *L. mitrocostatus*, is based on indeterminate material and is a *nomen dubium* restricted to the type specimen.

ONE of the most productive localities for Jurassic continental microvertebrates is the lignite mine of Guimarota, near the town of Leiria in Portugal (Kühne 1968). Until recently, the Guimarota lignites were generally interpreted as Lower Kimmeridgian (Upper Jurassic) in age on the basis of the ostracode assemblage (Helmdach 1971a, 1971b, 1973). However, the plant material suggests a Bathonian to Oxfordian age (Brauckmann 1978), and recent palynostratigraphical studies in the Iberian Peninsula unequivocally support an age not later than Oxfordian for the Guimarota coal seams (Mohr and Schmidt 1988; van Erve and Mohr 1988; Mohr 1989).

The Guimarota lignites are believed to have been laid down in swamps in an upper coastal plain with slight marine influence (Mohr 1989, p. 293). They have yielded a rich assemblage of microvertebrates, including fishes, amphibians, reptiles, and mammals, represented by both dissociated and associated skeletons. Among the lower tetrapods are abundant lizards or lizard-like forms which were described by Seiffert (1973) as scincomorphs (*Saurillus*, *Becklesisaurus*), an anguimorph (*Introrsisaurus*), and a new atypical anguimorph which Seiffert called *Lisboasaurus* and which he suggested might be an aigialosaur/mosasaur relative. As described, *Lisboasaurus* was represented by a small number of jaw fragments and isolated teeth which Seiffert divided between the type species *L. estesi* and a referred species *L. mitrocostatus*. Estes (1983, pp. 116, 118, 133) reassessed all Seiffert's taxa, transferring the Guimarota *Saurillus* and *Becklesisaurus* species to the new genera *Saurillodon* and *Becklesius* respectively; and transferring *Introrsisaurus* to the anguimorph genus *Dorsetisaurus*. Estes (1983, p. 193) removed *Lisboasaurus* from the Anguimorpha and categorized it as *Lacertilia incertae sedis*, with the comment that the holotype maxilla of *L. estesi* had some similarities to those of saurischian dinosaurs.

One of the authors (S.E.E.) has recently reexamined all the material of both species of *Lisboasaurus* in the collections of the Freie Universität, Berlin (= FUB), and the following redescription elaborates on the conclusions of Estes (1983).

SYSTEMATIC PALAEONTOLOGY

Superorder ARCHOSAURIA Osborn, 1902

Order SAURISCHIA Seeley, 1888

Suborder THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

MANIRAPTORA Gauthier, 1986

?AVIALAE Gauthier, 1986 *incertae sedis*

Genus *Lisboasaurus* Seiffert 1973

Type species. *L. estesi* Seiffert 1973.

Diagnosis. A small relative of troodontids and *Archaeopteryx* with the following characters: maxilla bearing large pit or diastema in the anterior tooth-row; maxilla with antorbital fossa, but with accessory antorbital fenestra absent or posteriorly placed; maxilla with slender dorsal process excluded from narial margin by tall ascending process of premaxilla; teeth with mediolaterally compressed triangular crowns with lingual groove, expanded roots wider than crowns and with 'waist' between crown and root; teeth with anterior and posterior carinae but no serrations.

Lisboasaurus estesi Seiffert, 1973

Text-figures 1–3.

1973 *Lisboasaurus estesi* Seiffert p. 33, fig. 27.

1983 *Lisboasaurus estesi* Seiffert; Estes p. 193, fig. 54A.

Holotype. FUB Gui.37, a nearly complete right maxilla about 22 mm long and bearing one tooth (Text-figs 1, 2A–D). Subsequent to the reexamination by S.E.E., and prior to photography, the holotype specimen was cleaned of residual matrix and apparently suffered damage to the wall of the antorbital fossa and the posterior end of the tooth-row. The photographs in Text-figure 1 depict it in this condition, while Text-figure 2A–C depicts the lost regions with broken lines.

Diagnosis. As for genus, this being the only valid species.

Locality and horizon. Guimarota lignite mine, 1.5 km SSE of Leiria, Portugal; Guimarota complex of lignitic marls, Oxfordian, Upper Jurassic.

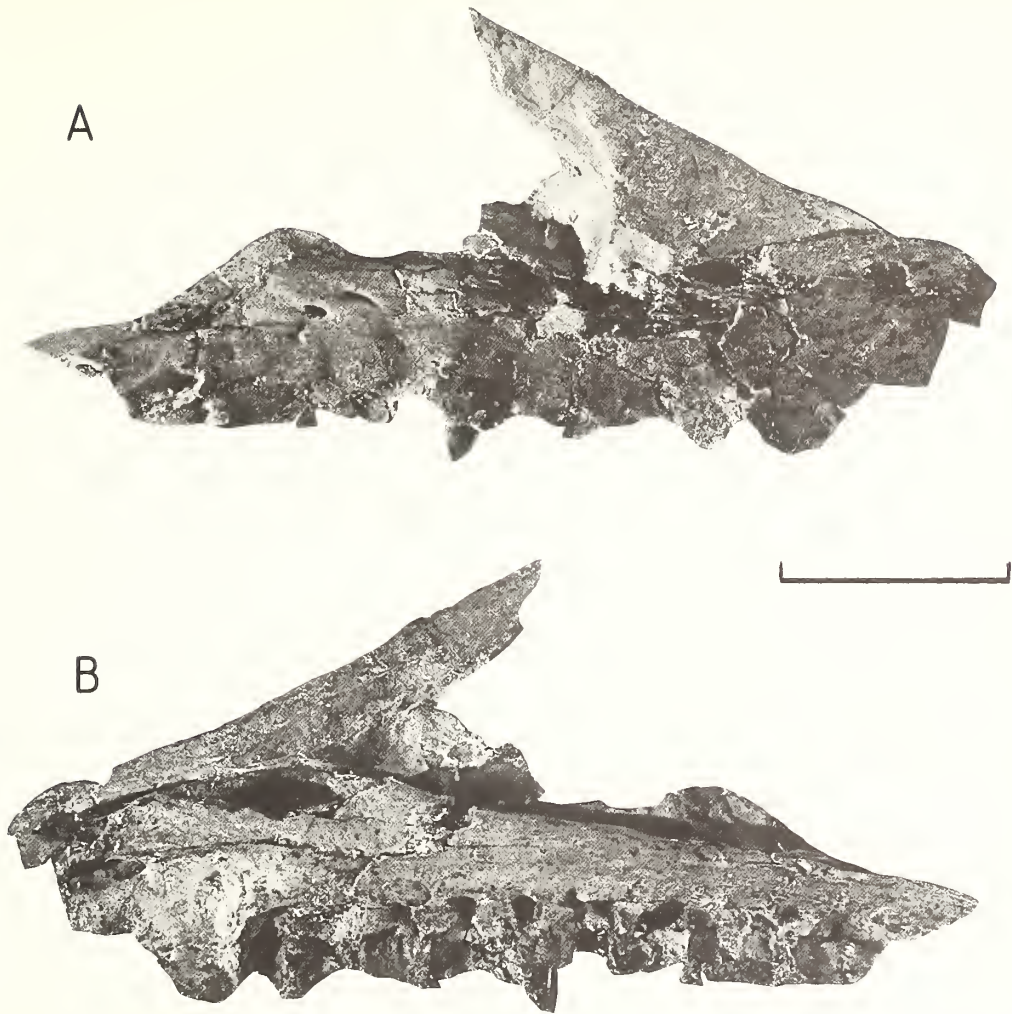
Referred material. A larger left maxilla (FUB field batch no. Jun. 81:13:1; Text-fig. 3A–C) and several isolated teeth (including FUB Gui.L. 136, Text-fig. 2E–F) are the only specimens that can certainly be referred here.

In addition to the above jaw material of *L. estesi*, Seiffert referred to it two small blocks containing associated skull and postcranial material (FUB Gui.L. 33 and L. 177). The preservation of this material is very poor. On the basis of these specimens, Seiffert stated that *Lisboasaurus* had procoelous vertebrae and fused frontals. However there is nothing on these blocks to link them positively with either the holotype maxilla or the referred teeth, and they are not treated as part of the hypodigm of *L. estesi* in the following description and discussion.

Description

The holotype maxilla (Text-figs 1, 2A–C) is short, with a long obliquely-sloping anterior border which is faceted and therefore did not enter the border of the external naris. The presence of a tall ascending process on the premaxilla is implied. The dorsal process of the maxilla is slender and probably only contacted the nasal weakly. The anterior tip of the maxilla is eroded, but there is no evidence that it bore a premaxillary process extending below the naris. The surface of the bone is excavated laterally to give a smooth-walled depression. Seiffert (1973) described this as an anteriorly shifted prefrontal facet, but it is too smooth to be a facet and is the antorbital fossa as noted by Estes (1983). The depression had a thin medial wall (lost after recent preparation), but its borders were damaged so that the shape of the fenestra, which must have lain further back, cannot be reconstructed. No accessory fenestrae are visible in the preserved portion of the fossa wall. Medially this part of the maxilla bears another, shallower depression (Text-fig. 2B) which could be part of a maxillary sinus. This sinus occurs in a comparable position in the maxilla of *Troodon* (Text-fig. 4).

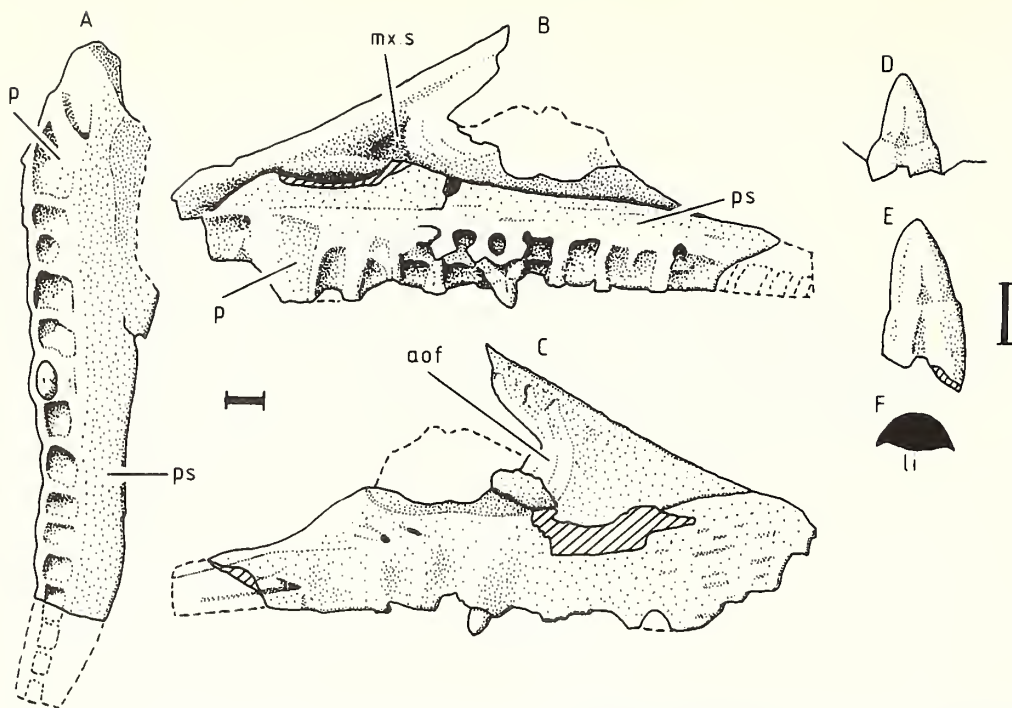
In the holotype maxilla, the dorsal process is separated from the alveolar region by a broad palatal shelf, widest anteriorly, although the medial edge is broken (Text-fig. 2A). Below it, the teeth sat in a deep groove, separated from one another by low ridges of interdental bone. There are spaces for about 13–14 teeth, but the maxilla may be incomplete posteriorly. One tooth is preserved intact (Text-fig. 2b) and its shape, unique in the context of known Jurassic microvertebrates, can be matched by a further set of isolated teeth (e.g. FUB Gui.L. 136 in Text-figure 2E). The teeth have mediolaterally compressed triangular crowns with anterior and posterior carinae. The labial surface is more rounded than the lingual one so that, in cross-section (Text-fig. 2F), the carinae appear to curve lingually. There are no serrations. The lingual surface is marked by a basal



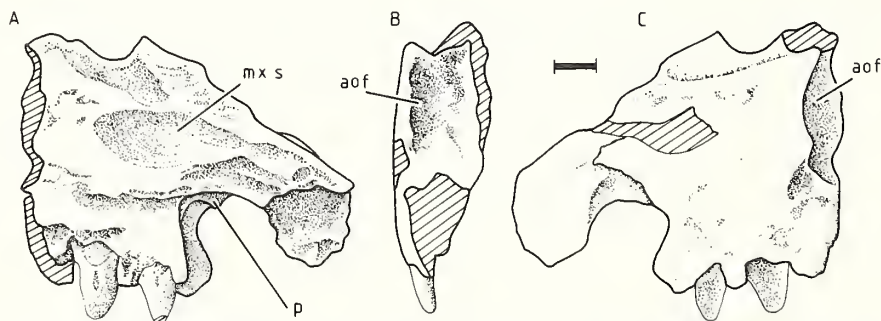
TEXT-FIG. 1. *Lisboasaurus estesi* Seiffert, holotype right maxilla FUB Gui. 37 in A, labial, and B, lingual aspects. Scale bar, 5 mm.

pit which gives rise to a shallow groove that extends towards, but does not reach, the tooth tip. The groove is visible only on the lingual sides of teeth in both maxillary specimens and so the lingual-labial orientation of isolated teeth is not in doubt. The crown is supported by an expanded root which is broader than the crown and there is a clear 'waist' between the two. In the holotype, the root is just visible in the sole preserved tooth which appears to be a partly erupted replacement tooth. This tooth is held in place by a low lingual wall of bone which may represent either a remnant of the alveolar wall or a weak development of this feature. Thus the implantation is thecodont. The expansion of the roots suggests that the roots fully enclosed the replacing teeth.

At the anterior end of the tooth-row of the holotype maxilla, there is a large pit, subdivided into two parts. The smaller anterodorsal section receives the opening of the superior alveolar canal (also visible in the maxilla of *Troodon*, Text-fig. 4). The larger pit is more problematical. It is too smooth to be a facet, or a socket for a large upper caniniform tooth (as suggested by Seiffert 1973 and Estes 1983). It appears to be a true diastema, probably a recess for reception of a lower caniniform tooth.



TEXT-FIG. 2. *Lisboasaurus estesi* Seiffert. A–C, holotype right maxilla FUB Gui. 37 in A, palatal, B, lingual, and C, labial aspects. D, Maxillary tooth from FUB Gui. 37 in lingual aspect (inverted for comparison with Gui. L. 136). E, F, Referred isolated tooth FUB Gui. L. 136 in E, lingual aspect, and F, cross-section of crown. All scale bars, 1 mm. Abbreviations: aof, antorbital fossa; li, lingual; mx.s, possible maxillary sinus; p, anterior pit; ps, palatal shelf.

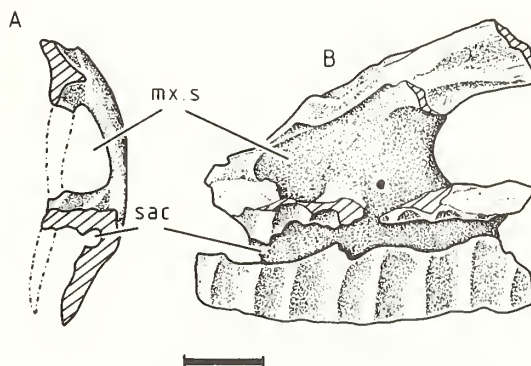


TEXT-FIG. 3. *Lisboasaurus estesi* Seiffert, referred left maxilla (FUB field batch no. Jun. 81:13:1) in A, lingual aspect, B, posterior view into anterior wall of antorbital fossa, and C, labial aspect. Scale bar, 1 mm. Abbreviations as in Text-figure 2.

A search through uncatalogued FUB material from Guimarota yielded a second incomplete maxilla (field batch no. Jun. 81:13:1) – a left element somewhat larger than the holotype specimen. This specimen (Text-fig. 3A–C) confirms most features of the holotype – antorbital fossa (Text-fig. 3B–C), maxillary sinus (Text-fig. 3A), anterior pit (Text-fig. 3A), tooth shape and thecodont implantation – and suggests that the holotype maxilla belonged to a juvenile. The thin outer wall of the anterior pit has broken away to give the appearance of a large notch in the tooth-row (Text-fig. 3C). This referred specimen differs from the holotype in one respect, namely

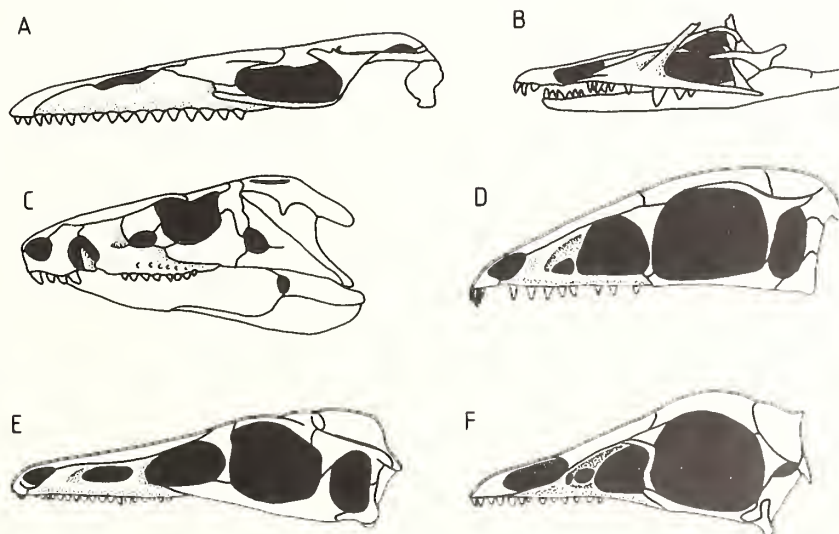
that there is considerably more alveolar bone, particularly along the lingual side of the jaw (Text-fig. 3A) so that the teeth are entirely in sockets. Whether or not this lingual bone was formed from interdental plates is impossible to determine because of the poor preservation of the specimen. The difference between the two specimens of *Lisboasaurus estesi* may reflect the ontogenetic development of the alveolar wall or could simply be due to greater post-mortem damage to the holotype.

TEXT-FIG. 4. *Troodon formosus* Leidy, right maxilla in A, reconstructed cross-section (redrawn after Currie 1985, fig. 2) and B, lingual aspect. Scale bar, 10 mm. Abbreviations: mx.s, maxillary sinus; s.a.e., superior alveolar canal.



Systematic position

The holotype maxilla of *L. estesi*, with its long ascending process, antorbital fossa and thecodont tooth insertion, clearly belongs to a small archosaur and not a lepidosaur (see Text-figure 5A for a mosasaur maxilla). Resemblances can be found to the maxillae of several groups of archosaurs with small Jurassic representatives, notably pterosaurs, primitive crocodylomorphs and higher maniraptoran theropods (troodontids and birds). Because the specimens are small and plausibly juvenile, they probably lack the allometric features of larger archosaurs of different groups and tend to have a phenetic resemblance to primitive pterosaurs and primitive crocodylomorphs, most of which occurred significantly earlier than *Lisboasaurus*.



TEXT-FIG. 5. Lateral views of the skulls of A, the mosasaur *Chidastes*; B, the pterosaur *Preondactylus*; C, the crocodylomorph *Protosuchus*; D, the theropod *Compsognathus*; E, the troodontid *Saurornithoides*; and, F, *Archaeopteryx*. (Drawings after A, Russell 1967; B, Wild 1983; C, Crompton and Smith 1980; D, Ostrom 1978; E, Russell 1969; F, Wellnhofer 1974.)

Pterosauria. The maxilla of *L. estesi* resembles that of some rhamphorhynchoid pterosaurs (e.g. the Norian *Preondactylus* Wild 1983) in its long anterodorsal process and the possible presence of a caniniform tooth (Text-fig. 5B). However in rhamphorhynchoids, the caniniform tooth is not at the anterior end of the tooth-row, but in the middle, and is separated from the tip of the bone by a long slender process bearing a further series of small teeth. This does not appear to be the condition in *L. estesi*. There are further differences. In *Lisboasaurus*, the dorsal process is faceted and was probably excluded from the narial margin, unlike that of any described rhamphorhynchoid, although the character is present in pteranodonts. The rhamphorhynchoid maxilla is slender and lightly-built and it lacks an antorbital fossa set in the front of the fenestra. Tooth shape also differs; pterosaurs do not have the combination of waisted teeth and sharply expanded roots. One Upper Jurassic genus, *Germanodactylus*, does have teeth with short triangular crowns each with a groove running down one side (Wellnhofer 1970, pl. 10, fig. 2, and D. M. Unwin pers. comm.) but the groove is labial, not lingual as in *Lisboasaurus*, and the maxilla of *Germanodactylus* is of very different shape. In conclusion, *Lisboasaurus* might be an aberrant pterosaur, but as will be argued below, its total suite of characters suggest a closer resemblance to another group.

Crocodylomorph and avialan teeth. Martin *et al.* (1980) and Martin (1983b) noted the resemblance of crocodile and Mesozoic bird teeth and suggested that they indicated immediate relationship. Most other workers accept the characters but treat them as convergent (e.g. Gauthier 1986). The teeth of *Lisboasaurus estesi* bear a distinct resemblance to the crocodile-Mesozoic bird tooth type in that they possess expanded roots, waists, and non-serrate carinae. The only group in which these teeth occur in combination with a large antorbital fenestra, are the primitive crocodylomorphs of the sphenosuchian grade and the higher maniraptoran theropod dinosaurs of the Troodontidae and Avialae (birds and relatives).

Crocodylomorpha. At least four genera of crocodile are known from Guimarota, comprising *Machimosaurus*, *Goniopholis*, a *Theriosuchus*-like form, and a *Bernissartia*-like form (Brinkmann 1989). All are typical crocodylomorphs in that they have very reduced or no antorbital fenestrae, and are thus distinct from *Lisboasaurus*. However, members of the primitive pre-crocodyliform grade of crocodiles retain a relatively large fenestra. Most of these are Upper Triassic or Liassic in age, but one, *Hallopus victor*, is from the Upper Jurassic of Colorado (Walker 1970) and hence contemporaneous with *Lisboasaurus*. The only specimen of *Hallopus* lacks cranial material, so comparison must be made with Upper Triassic and Liassic genera. Unfortunately, most of these are represented by specimens which are considerably larger than *Lisboasaurus* and so comparisons of shape are difficult.

The recent evaluation of primitive crocodylomorph relationships by Benton and Clark (1988) places the well-characterized primitive crocodylomorphs in two grades. The basal grade includes *Saltoposuchus* (= *Terrestrisuchus* of Crush 1984). The '*Terrestrisuchus*' material described by Crush (1984) has a much more elongate maxilla than *Lisboasaurus* with an anteroposteriorly long dorsal ramus. The teeth of *Terrestrisuchus* are flattened like those of *Lisboasaurus* but are recurved and serrated. Neither maxilla nor teeth of *Terrestrisuchus* could be confused with *Lisboasaurus* material.

Slightly more advanced crocodylomorphs include the sphenosuchids *Sphenosuchus* and *Hesperosuchus* and the aberrant *Platygnathus*. *Sphenosuchus* and *Hesperosuchus* have teeth with compressed lanceolate crowns, waists and cylindrical roots (Walker 1970, p. 348, fig. 12) which resemble those of *Lisboasaurus*. The teeth of *Sphenosuchus* are serrated, while *Platygnathus* has unique recurved teeth with a polygonal cross-section and a serrated posterior edge (Simmons 1965, pp. 35, 39–40). Unlike *Lisboasaurus*, these Triassic-Liassic forms possess a maxilla with an anteroposteriorly long dorsal process and a posteriorly set fossa associated with the elongate anterior muzzle. *Sphenosuchus* and *Platygnathus* both possess a large anterior mandibular fang which fits into a deep notch in the upper jaw, but in both genera, the notch is at the premaxilla-maxilla junction and not a pocket within the maxilla as in *Lisboasaurus*. This condition is shown well in the more advanced *Protosuchus* (Text-fig. 5c), as described by Crompton and Smith (1980). Thus the teeth of *Lisboasaurus* share some characteristics with those of early crocodylomorphs, but the maxilla shows no special similarity.

Maniraptoran Theropoda. The term Maniraptora was created by Gauthier (1986, p. 30) to define a clade of bird-like theropod dinosaurs and birds. The group, as defined by Gauthier, comprises *Compsognathus* and several minor 'coelurosaurs', the families Caenagnathidae, Elmsauridae, Dromaeosauridae, Troodontidae, and the Avialae (*Archaeopteryx* and all birds). Gauthier (1986) suggested that the Dcinyonchosauria (Dromaeosauridae + Troodontidae) were the sister-group of the Avialae, but Currie (1987) has argued that the Troodontidae alone are the immediate sister-group of the Avialae, and noted some derived characters which the two groups share uniquely within the Theropoda. The characters of *Lisboasaurus* relate largely to the

troodontid-avialan clade which at present has no name. For the purposes of this discussion, the Troodontidae is taken to comprise the genera *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, and *Borogovia* (for recent reviews, see Currie 1987 and Osmólska 1987). All these genera are from the Upper Cretaceous, but if Currie (1987) is correct in arguing that the troodontids are the sister-group to the Avialae then there must have been at least stem-troodontids in the Upper Jurassic, contemporaneous with *Archaeopteryx*.

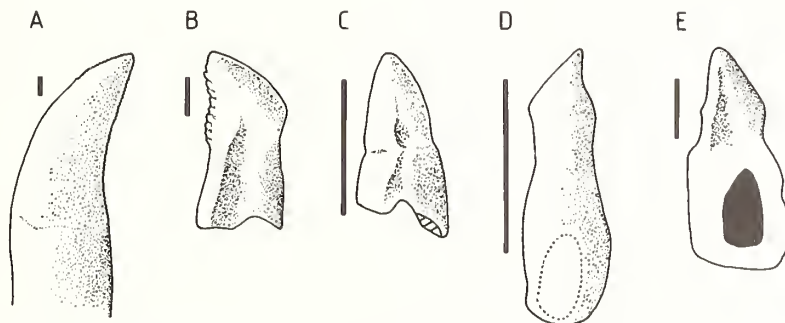
The maxilla of *Lisboasaurus* is very similar in shape to those of small maniraptorans, such as *Compsognathus* (Text-fig. 5D) and *Archaeopteryx* (Text-fig. 5F). As noted in the description, the anterior maxillary teeth of *Lisboasaurus* have compressed asymmetrical cross-section with rounded labial and flattened lingual surfaces and the carinae on the lingual corners. Currie (1987, p. 77) noted this to be a character of the premaxillary teeth of theropods, and it would not be surprising if it extended to the anterior maxillary teeth. Compressed asymmetrical crowns of this type also occur in *Archaeopteryx* (Howgate 1984b, p. 656), but carinae are not visible (P. Wellnhofer pers. comm.). The following characters are discussed in the context of the Maniraptora. The condition in troodontids is taken from Currie (1987) and the condition in *Archaeopteryx* is taken from Howgate 1984a, b, and Wellnhofer (pers. comm.).

The following derived character is shared by troodontids, *Archaeopteryx*, and *Lisboasaurus*.

- A. Teeth with constriction between crown and root (Text-fig. 6B–E *contra* the primitive theropod condition, e.g. *Megalosaurus* in Text-fig. 6A).

The following derived character is shared by *Archaeopteryx* and *Lisboasaurus*, but not troodontids.

- B. Teeth completely unserrated (Text-fig. 6C–D; Gauthier 1986, p. 12).



TEXT-FIG. 6. Archosaur teeth in lingual aspect. A, *Megalosaurus bucklandi* (original from mandible of holotype, British Museum (Natural History) R.332; serrations present but not visible at this scale); B, *Troodon* (after Currie 1987); C, *Lisboasaurus*; D, *Archaeopteryx* (after Howgate 1984b); E, hesperornithid (after Martin 1983a). Scale bars, 10 mm (A) and 1 mm (B–E).

Compsognathus lacks serrations on the premaxilla and anterior dentary teeth, but these teeth are recurved, slender-crowned, and also lack carinae. The maxillary teeth of *Compsognathus* have carinae, the posterior carina being serrated (Ostrom 1978). (*Archaeopteryx* and *Lisboasaurus* also share some primitive features *contra* troodontids. They appear to retain a maxillary tooth count of 12–15, whereas troodontids have 19–20 maxillary teeth, but the latter is probably the derived condition. Unlike troodontids, both *Archaeopteryx* and *Lisboasaurus* retain the antorbital fossa, but Gauthier (1986) described this character state as primitive for archosaurs.)

The following derived character is shared by *Lisboasaurus* and troodontids but is not known in *Archaeopteryx*.

- C. Maxillary teeth each have a depression at the base of the lingual side of crown which extends as a groove towards the crown tip but does not reach it (Text-fig. 6B–C).

(There are other differences of uncertain polarity in the shape of the crowns, those of *Archaeopteryx* being more recurved (Howgate 1984a, b) than those of *Lisboasaurus*.)

The following derived characters are shared by *Lisboasaurus* and the Ornithurae (post-*Archaeopteryx* birds), but not troodontids or *Archaeopteryx*.

D1. Maxilla separated from naris by processes of premaxilla and nasal.

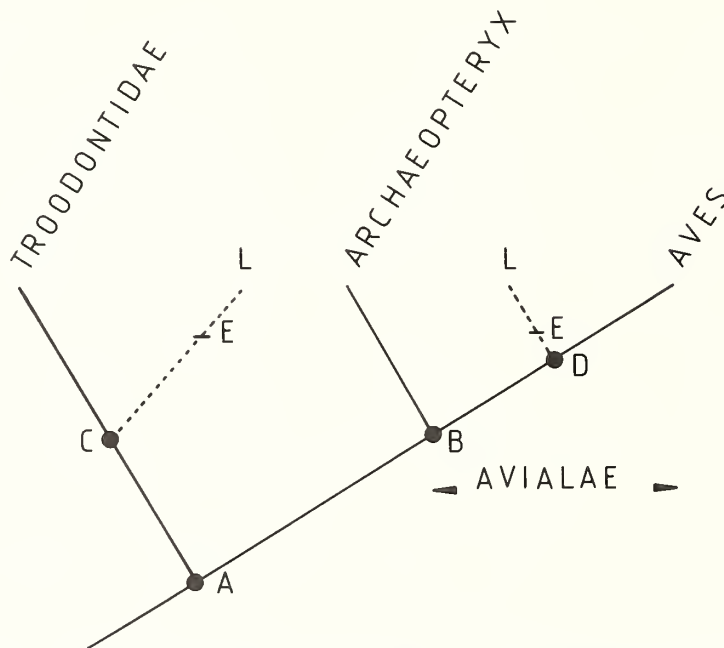
In *Archaeopteryx*, unlike *Lisboasaurus*, the anterodorsal process of the premaxilla is shorter and reconstructions show the maxilla entering the narial margin, a typical saurischian condition (Howgate 1984a). Gauthier (1986, p. 15) notes that exclusion of the maxilla from the naris occurs as the primitive thecodontian condition, is lost in Saurischia, but appears as a reversal in ornithomimids and ornithurine (post-*Archaeopteryx*) birds.

D2. Teeth with root wider than crown (Text-fig. 6C,E; Gauthier 1986, p. 12).

The following derived character occurs in *Lisboasaurus* but not in troodontids or *Archaeopteryx*.

E. Large pocket or diastema near anterior end of maxilla suggesting presence of a lower caniniform tooth.

Relationships. If *Lisboasaurus estesi* is a maniraptoran theropod, then character A places it in the troodontid-avialan clade, B places it within the Avialae, while in contradiction, C places it within the Troodontidae. D1 and D2 are weak (because variable) characters which suggest a post-*Archaeopteryx* position in the Avialae and E is a unique character in the context of a troodontid-avialan clade and serves as a defining autapomorphy for *Lisboasaurus*. Text-fig. 7 depicts the alternative relationships of *Lisboasaurus* suggested by these characters. This character distribution suggests that *Lisboasaurus* is a member of the troodontid-avialan clade and could be a primitive avialan. The implications and qualifications to this systematic position are discussed below in the discussion section.



TEXT-FIG. 7. Cladogram depicting the possible relationships of *Lisboasaurus* to troodontid dinosaurs, *Archaeopteryx*, and Aves. Character-states A-E are those described in the text. Abbreviation: L, *Lisboasaurus*.

A NOTE ON '*LISBOASAUROS*' *MITROCOSTATUS*

The material which forms the basis of this species is more problematical than that of *L. estesi*. The holotype dentary (FUB Gui. 34) is crushed, but appears to show a type of thecodont implantation essentially similar to that of *L. estesi*. The external surface of this dentary bears a pattern of striate sculpture which is unlike that of any lizard (Estes 1983). Some of the referred teeth resemble those of *L. estesi* but have a short rounded crown (e.g. FUB Gui. L. 67). Others, however, have a longer pointed crown (e.g. FUB Gui. 18 and 24). This variation suggests that more than one taxon may be represented – a possibility recognized by Seiffert (1970), when he

divided the *L. mitrocostatus* material into two subspecies. Estes (1983) suggested that at least some of the *L. mitrocostatus* material might be referable to the genus *Cteniogenys* which is also known from Guimarota (Seiffert 1973, pp. 13–17). *Cteniogenys* was originally described as a lizard but has recently been shown to be an early choristodere (Evans 1989, 1990). Although superficially similar, the striations on the jaw of *Cteniogenys* are created by a double row of sensory foramina, not the rather irregular sculpturing seen in the *L. mitrocostatus* holotype. The teeth and their mode of implantation are also different, and reference to *Cteniogenys* is highly unlikely. The *L. mitrocostatus* material is too limited to permit firm conclusions, but we agree with Estes (1983) that there is no certainty that the two species are congeneric. In conclusion '*Lisboasaurus*' *mitrocostatus* is, at present, a *nomen dubium* restricted to the holotype dentary, which is not sufficiently determinate to be associated with *L. estesi*, but certainly does not belong to *Cteniogenys* or a true lizard.

DISCUSSION

This study commenced as an assessment of the lacertilian status of *Lisboasaurus estesi*, and the unequivocal conclusion is that the *L. estesi* material is not lacertilian but represents a small archosaur. Our further conclusions must, of necessity, be circumspect for two reasons. The first is the limited nature of the material. Maxillae and teeth can only bear a restricted set of characters and some of these occur convergently in more than one group of small archosaurs. The resemblances of crocodile and Mesozoic bird teeth noted by Martin *et al.* (1980) and Martin (1983*a, b*) are generally agreed to be due to convergence (e.g. Gauthier 1986) but are clearly a source of uncertainty when limited material such as *Lisboasaurus* is being studied. However, parsimonious treatment of the available restricted suite of characters does lead to a position in the troodontid-avian clade with no character contradictions. A less certain parsimonious conclusion, because there is contradiction, is the position within the avialan clade.

A second reason for circumspection is that the early evolution of birds is both poorly known and subject to intense speculation. An Oxfordian relative of *Archaeopteryx* might be the earliest known bird, and yet there is nothing in the morphology of the *Lisboasaurus* fragments that has any bearing on the origin of birds or bird flight. It does, however, serve as a reminder that *Archaeopteryx* was probably only one of an array of similar smaller forms, including stem-troodontids. It is likely that most Jurassic microvertebrate assemblages will prove to contain maniraptoran material which cannot be securely identified as avian or non-avian, the recently described material from the late Jurassic Uncompahgre Formation of Colorado being a case in point (Jensen and Padian 1989). A more precise systematic position for *Lisboasaurus* must await the identification and description of further material from Guimarota.

It would not be too surprising if *Lisboasaurus estesi* were an *Archaeopteryx*-grade maniraptoran. The Solnhofen Limestone represents a coral lagoon floor of Lower Tithonian age (*circa* 150 Ma) in southern Germany. The Guimarota lignite represents a coastal swamp of probable Oxfordian age (*circa* 160 Ma) in Portugal. The two localities are about 1500 km apart and may have been about 1200 km apart in the Jurassic. The presence of similar proto-birds in two contemporaneous continental-coastal localities 1200 km apart within one continent could reasonably be expected.

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THE CONCHOSTRACAN FAUNA OF THE GREAT ESTUARINE GROUP, MIDDLE JURASSIC, SCOTLAND

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ABSTRACT. The Great Estuarine Group contains the most diverse conchostracan fauna so far described from the Jurassic or Cretaceous of Europe, comprising twelve species in seven genera. *Estheria munchisoniae* Jones was described in the last century; it is now referred to *Pseudograptia* Novojilov and is the youngest member (latest Bathonian?) of the fauna described here. *Euestheria trotternishensis* and *Neopolygrapta leatensis* spp. nov. occur near the base of the Great Estuarine Group and probably close to the Bajocian–Bathonian boundary. *Dendrostracus hebridesensis* sp. nov. occurs towards the top of the Kildonnán Member, Lealt Shale Formation. In the overlying Lonsearn Member, *Skyestheria intermedia* sp. nov. appears (probably descended from *Neopolygrapta*) and itself gives rise to *Antronestheria praecursor* sp. nov. The higher parts of the Great Estuarine Group, including most of the Kilmaluag Formation, are dominated by *Antronestheria kilmahuagensis* sp. nov., with one occurrence of *Fibrestheria puncta* sp. nov. The *Pseudograptia* fauna (containing *P. orbita* Chen, *P. morrisi* sp. nov., *P. jonesi* sp. nov. and *P. munchisoniae* (Jones)) occurs in beds probably near the top of the Kilmaluag Formation. All the conchostracans inhabited shallow, freshwater to oligohaline, near-coastal, lagoons. Biogeographic comparisons with China show that the earlier faunas were distinct in the two areas, but the *Pseudograptia* fauna occurs in both. Details of the construction of conchostracan growth bands are revealed by stereo scanning electron micrographs.

CONCHOSTRACANS are small, bivalved branchiopod crustaceans with a non-mineralized carapace. They occur in non-marine facies from the Devonian to the present day, sporadically but often in great abundance; many palaeontologists still refer to them informally using the pre-occupied generic name '*Estheria*'. Jurassic and Cretaceous conchostracans have been little studied in Europe, no doubt partly because of the limited occurrence of suitable facies, but they have been extensively studied in Siberia and China, where they are important biostratigraphically within thick successions of non-marine strata deposited in large internal basins (e.g. Sichuan basin, Sungliao basin: Chen and Shen 1985; general summary in English, Chen *et al.* 1982, pp. 1011–1014). It is therefore important to examine conchostracan faunas in Europe that can be accurately dated by intercalation within marine sections.

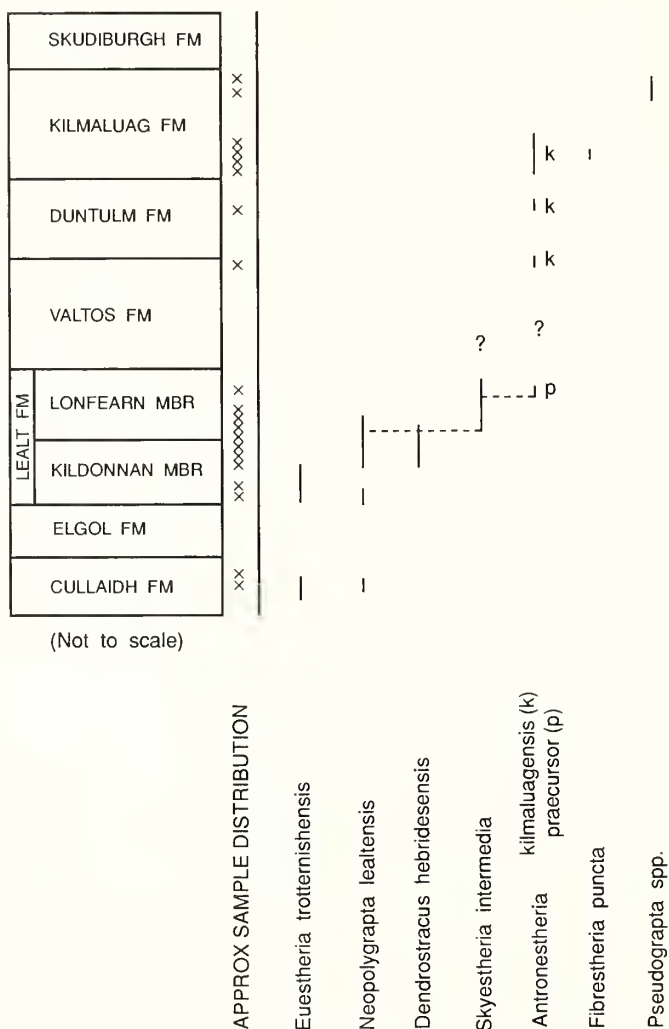
In Britain, conchostracans occur in the Triassic, including the Penarth Group ('Rhaetian'), sporadically in the Bathonian of central England, in the Purbeck Beds (top Jurassic-early Cretaceous) and in the Wealden Beds (early Cretaceous). By far the most abundant Jurassic faunas, however, are those of the Great Estuarine Group of the Inner Hebrides, NW Scotland, where conchostracans occur profusely, associated with the non-marine end of a series of faunal assemblages ranging from restricted-marine to freshwater (Hudson 1963*a*, 1963*b*, 1980). The age is late Bajocian–Bathonian. This occurrence is of interest from several points of view: local and worldwide biostratigraphical, palaeoecological, and palaeo-biogeographical. Our scanning electron microscope (SEM) studies have also enabled us to add important morphological details to existing knowledge of the conchostracan carapace, and we illustrate conchostracan sculpture stereoscopically for the first time.

THE GREAT ESTUARINE GROUP

The Great Estuarine Group is an intercalation of varied paralic facies, up to 270 m thick, in the otherwise marine Jurassic succession of the Minch Basin (Hudson 1983). Its lithostratigraphy has

been reviewed by Harris and Hudson (1980). The base of the Group is defined at the upward passage from ammonite-bearing clays of the *garantiana* zone (late Bajocian) into dark shales, with a restricted fauna, of the Cullaidh Shale Formation. Its top occurs where the non-marine Skudiburgh Formation is abruptly overlain by the Upper Ostrea Member of the Staffin Bay Formation; this is dated palynologically as no older than the *discus* zone (latest Bathonian), and is overlain by the Belemnite Sands Member, *macrocephalus* zone, early Callovian (Bradshaw and Fenton 1982). The Great Estuarine Group may therefore include equivalents of the latest Bajocian *parkinsoni* zone, but most of it must be Bathonian. It can be divided into several distinctive formations that can be correlated lithostratigraphically (Harris and Hudson 1980; see Text-fig. 1),

Stratigraphic Ranges of Conchostraca in the Great Estuarine Group



TEXT-FIG. 1. Stratigraphic subdivisions of the Great Estuarine Group (Harris and Hudson 1980), showing ranges of the main conchostracan species.

but no internal biostratigraphy is currently available. It seems likely, on grounds of regional event stratigraphy, that the Duntulm Formation correlates with the White/Blisworth Limestones of central England (Andrews 1985) and thus most probably with the *hodsomi* zone of the Bathonian (Torrens in Cope *et al.* 1980).

Within the Great Estuarine Group, the predominantly shale, low-salinity formations, especially the Lealt Shale Formation (both Kildonnan and Lonfearn Members) and the Kilmaluag Formation, contain abundant conchostracans. There are more limited occurrences in the Cullaidh Shale Formation, in the shale facies within the Valtos Formation, and in a freshwater intercalation within the Duntulm Formation. A definite stratigraphical arrangement of the conchostracan taxa emerges from our present sampling, and suggests that they will be useful in local and perhaps wider stratigraphical correlation.

PREVIOUS WORK ON CONCHOSTRACANS FROM THE GREAT ESTUARINE GROUP

Jones (1863) described the species *Estheria murchisoniae* from Skye; this was subsequently made the type species of the genus *Pseudograptia* Novojilov, 1954. No systematic descriptions or illustrations have appeared since, although conchostracans have been recorded from the Great Estuarine Group many times, variously as *Estheria*, *Euestheria* or *Cyzicus*, and gave their name to the Estheria Shales of Anderson (e.g. Anderson and Dunham 1964), now the Lealt Shale Formation of Harris and Hudson (1980). Hudson (1963b, p. 337) recorded conchostracans from several horizons within the Group and reported that 'each sample was reasonably homogeneous within itself, but that there was considerable variation between samples, especially in interspace ornament and also in size'. This suggested that several taxa were present, but in view of the then-prevailing confusion in conchostracan taxonomy, Hudson retained all the specimens in Jones's species *murchisoniae*, which he referred to *Euestheria* Deperet and Mazeran.

MATERIAL STUDIED

In 1988 we made two visits to the Hebrides specifically to collect material for this paper. We have also made extensive use of collections made by Hudson since 1963, in the collections of the Leicester University Geology Department, and between 1956–62, in the Sedgwick Museum, Cambridge. All material from the Great Estuarine Group used for this paper is listed in an Appendix, which is deposited at the British Library as Supplementary Publication No. SUP 14039 (11 pages). We have also re-studied the specimens described by Jones (1863) at the British Geological Survey, Keyworth, a limited amount of Geological Survey material from southern England, and some core material loaned by British Petroleum plc from the Porcupine Basin. Chen has made extensive use of the collections of the Nanjing Institute of Geology and Palaeontology for comparative purposes, and some material collected jointly in China in 1989, or presented to Hudson by Chen, is now in the Leicester University collections.

DISTRIBUTION OF CONCHOSTRACAN FAUNAS

The stratigraphy of the Great Estuarine Group and the distribution of conchostracans within it are summarized in Text-figure 1.

Lealt Shale Formation and Cullaidh Shale Formation

Stratigraphy. It is convenient to consider the two lowest shale formations together, because from the point of view of conchostracan distribution the unfossiliferous Elgol Sandstone Formation can be regarded as an intercalation within them. We have sampled the Cullaidh Shale Formation and the basal part of the Kildonnan Member of the Lealt Formation at two localities each. The middle part of the Kildonnan Member contains few, if any, conchostracans. Its upper part contains many,

and they continue into the lower part of the Lonfearn Member, which we have also sampled at several localities. The upper part of the Lonfearn Member contains conchostracans, but we have not sampled it adequately, and the same applies to the sparse conchostracan fauna of the basal Valtos Formation above.

In the Cullaidh Shale and basal Kildonnan Member, the genera *Euestheria* and *Neopolygrapta* occur, each represented by one species (when specifically identifiable). *Euestheria* is confined to these basal beds, except for one occurrence in the higher part of the Kildonnan Member, at which horizon *Neopolygrapta lealtensis* sp. nov. is joined by *Dendrostracus hebridesensis* sp. nov. These two species continue into the basal part of the Lonfearn Member, but have not been found more than about 3 m above the algal limestone that marks the contact between the members. Before the disappearance of *Neopolygrapta*, *Skyestheria* appears. Morphological features suggest it may have evolved from *Neopolygrapta*. *Skyestheria* is the commonest conchostracan in the middle part of the Lonfearn Member, including the shales in the Lealt River (immediately above and below a limestone with *Chara* fragments) from which conchostracans have most often been collected in the past. *Neopolygrapta* also occurs here. (This locality is mentioned in Hudson 1963b, p. 339; note that the new road bridge is a few metres upstream of the old one and stands on what were formerly the best exposures.)

A few metres higher, *Antronestheria praecursor* sp. nov. appears in abundance (noted as 'form with punctate ornament' by Hudson 1963b, p. 339). It probably evolved from *Skyestheria* and itself leads to *Antronestheria kihnuhagensis* sp. nov., which dominates the faunas of the higher Great Estuarine Group. Our data are insufficient to show whether or not *Skyestheria* and *Antronestheria* overlap stratigraphically. The species *Skyestheria elliptica* sp. nov. is only known from one sample; its horizon within the Lonfearn Member is unknown, but likely to be near the middle because of the occurrence of oolitic limestones nearby.

Palaeoecology. The Cullaidh Shale Formation has a sparse fauna mainly of fish scales and tiny gastropods, with occasional occurrences of bivalves including mytilids. We do not have sufficient information to relate the conchostracan occurrences to the rest of the fauna, which is clearly not a normal marine one. In the Raasay section, conchostracans occur near the passage into the Elgol Sandstone Formation and not in association with the marine-brackish faunas recorded by Forsyth (1960) from stratigraphically lower.

In the Lealt Shale Formation conchostracans occur with the freshwater gastropods *Viviparus* and *Valvata* and the bivalve *Unio*, as well as commonly (from its incoming in the higher Kildonnan Member upwards) with the probably freshwater-brackish bivalve *Neomiodon*. The commonest associates of the conchostracans are freshwater to oligohaline ostracods of the genera *Limnocythere*, *Darwinula* and *Theriosynoecium*, with less commonly the euryhaline genus *Micropneumatocythere*. In the type section of the Kildonnan Member, Eigg, conchostracans do not occur in Beds 3–5 (Hudson 1966 and unpublished data) which are dominated by the brackish-water bivalve *Praemytilus strathairdensis*, nor in association with the marine-brackish *Placumopsis-Cuspidaria* faunas that occur in both members of the Formation. Walton (pers. comm. 1988) finds an excellent correlation between the proportion of the planktonic alga *Botryococcus* in palynological preparations and the presence of freshwater to oligohaline indicators (including conchostracans) in the macrofauna. In one bed in the Lonfearn Member in Trotternish (bed 1 of Hudson 1963b, p. 339) *Skyestheria* co-occurs with small mytilid bivalves. In general, the new data confirm that conchostracans inhabited the freshwater-brackish end of a spectrum of coastal lagoons of varying salinity (Hudson 1963a, 1963b, 1980; see also Tasch 1987, p. 139). Details will no doubt emerge from further collecting and from work in progress on the ostracod faunas and the palynology.

Valtos and Duntulm Formations

Few horizons in these formations yield conchostracans. We have studied only two samples, a bed 0.47 to 0.32 m below the top of the Valtos Formation on Muck, overlying a conspicuously yellow-weathering dolomitic limestone (Andrews and Walton 1990, p. 13, fig. 10), and Beds 6–7 of the

Duntulm Formation at Lon Ostaoin, Skye (the 'freshwater intercalation' of Andrews and Walton 1990, p. 8). Both yield *Antronestheria kihmahuagensis*, accompanied by *Neomiodon* and, in Muck, *Darwinula*.

Kihmahuag Formation

Stratigraphy. Conchostracans occur very commonly in the Kilmaluag Formation, wherever suitable lithologies (shales or fissile argillaceous limestones) are developed. With the exception of three localities, all the conchostracans belong to *Antronestheria kihmahuagensis* gen et sp. nov. This has been identified from the type section at Kilmaluag (beds 1, 3, 6, 7), bed 8 from Lon Ostaoin, and bed 4 from Prince Charles's Point; all bed numbers from Andrews (1985, p. 1122). Other Skye localities include the shore near the mouth of Lon Sgapail (Andrews, 1985, p. 1334), cliffs near Osmigarry (NG 390719), and slipped blocks on the shore of Lub Score (NG 404728). These occurrences span most of the exposed section of the Kilmaluag Formation, those at Kilmaluag being in its lower part and that at Prince Charles's Point probably in its upper part (Andrews 1985, p. 1134). In Strathaird, the Kilmaluag Formation is too metamorphosed to yield identifiable conchostracans. *A. kihmahuagensis* is abundant in its lower part at Laig Gorge, Eigg (beds 1, 2, 3, 5, 9 of Andrews, 1985, p. 1125).

One sample from bed 7 at Kilmaluag yielded the only other conchostracan species so far known from this horizon, *Fibresteria pincta* sp. nov. Other samples from this bed yielded only *Antronestheria*. *Fibresteria* also occur in the Blisworth Limestone of central England (see below).

Two localities have yielded a totally different conchostracan fauna consisting of species of *Pseudograptia* Novojilov. From one of these came the original material of *Estheria munchisonae* Jones: 'Mugstok' (Monkstadt), Trotternish (a locality also referred to as 'Icolmkill'). The specimens were collected by Murchison in 1826 from a temporary exposure made during the drainage of the former Loch Chaluim Cille, probably approximately NG 375695. Murchison (1829, p. 311) recorded, in blue shale, '*Ammonites Koenigi*, *Ostracae* in masses, many belemnites, flattened Tellinae (?), etc.' The 'flattened Tellinae' are the conchostracans subsequently described by Jones (1863), and preserved in the Geological Society Collections, now at the British Geological Survey, Keyworth, as No. 7296. The lithology, fine-grained grey argillaceous limestone with conchostracans almost covering one bedding plane, resembles typical Kilmaluag Formation. It is impossible to be sure how close the association with the other fauna recorded by Murchison was, but the presence of oysters suggests the Upper *Ostrea* Member, and the belemnites and ammonites the Belemnite Sands Member, both of the Staffin Bay Formation (Sykes 1975). It therefore seems most probable that the conchostracans occurred high in the Kilmaluag Formation or conceivably as an intercalation of 'Kilmaluag' facies within the Skudiburgh Formation.

The other *Pseudograptia* locality is in the Kilmaluag Formation of Muck, beds 13, 14 and 15 of Andrews (1985, p. 1125). Abundant and well preserved conchostracans occur in argillaceous dolomites, without macrofauna or ostracods. This outcrop is tectonically separated from the nearby Duntulm Formation and overlain by Palaeocene agglomerate. Lithological comparison with Strathaird suggests a high horizon with the Kilmaluag Formation (Andrews, 1985, p. 1128). Our suggestion, therefore, is that the *Pseudograptia* fauna is younger than the *Antronestheria* fauna and both are late Bathonian. At both localities *Pseudograptia munchisoniae* is accompanied by the species *P. orbita* Chen and *P. jonesi* sp. nov.; the Muck locality additionally yields *P. morrissi* sp. nov.

Palaeoecology. As in the Lealt Shale Formation, the occurrence of conchostracans in the higher Great Estuarine Group clearly correlates with non-marine facies, and it is likely that the Kilmaluag Formation lagoons were only tenuously connected to the open sea (Andrews 1985). *Antronestheria kihmahuagensis* is nearly always accompanied by ostracods (*Theriosynoecum*, *Darwinula*) that are considered to be freshwater or oligohaline (Kilenyi in Tan and Hudson 1974, p. 107); the *Theriosynoecum* show variations in node development. These forms are often accompanied by *Klieana*, which can also tolerate higher salinities. Some horizons additionally contain the brackish-marine ostracod *Progonocythere* (M. Wakefield pers. comm. 1989). Other associated fossils are

Viviparus, *Chara* oogonia, fish fragments and cuticular fragments of higher plants. The occurrence of *Pseudograptia* in ostracod-free dolomites from Muck may suggest tolerance of evaporated water and perhaps elevated (but non-marine) salinities by this genus (cf. Andrews *et al.* 1987). The Skye occurrence is in limestone, not dolomite (checked by X-ray diffraction), and also lacks associated ostracods, as do the occurrences of *Pseudograptia* spp. in Liaoning Province, China.

Bathonian of Southern and Eastern England

We have examined conchostracans from three localities in the Bathonian of England, using material from the BGS collections, Keyworth. Those from the top part of the Blisworth Limestone of Newport Pagnell, Bucks., may be assigned to *Fibrestheria* cf. *puncta* sp. nov. The horizon is probably late Bathonian and about the same age as the occurrence of *F. puncta* in the Kilmaluag Formation, Skye. An occurrence in the Forest Marble near Cirencester is of poorly preserved specimens of *Dendrostracus*? This horizon is also late Bathonian, and if the occurrence is confirmed it will probably represent a later occurrence of *Dendrostracus* than in the Hebrides, where it is confined to the Lealt Shale Formation of probable early to mid Bathonian age. The Blisworth Clay of the Nettleton Bottom borehole yields *Autronestheria kilhualuagensis* and is probably of similar age to the Kilmaluag Formation, late Bathonian. Locality details of the English occurrences are given in the systematic section below.

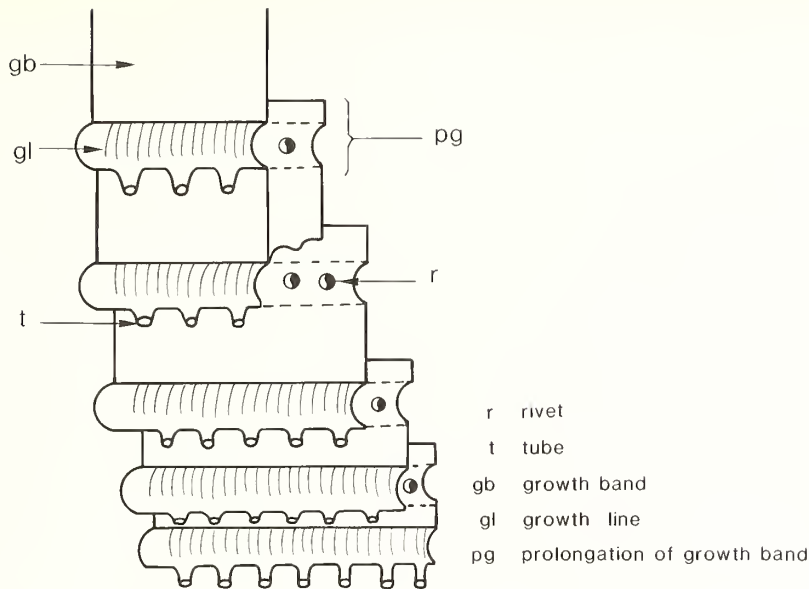
Porcupine Basin

A particularly interesting record of *Autronestheria kilhualuagensis* is in material loaned to us by the British Petroleum Company plc from a core taken in the northern part of the Porcupine Basin, offshore SW Ireland. The fossils and lithology are indistinguishable from typical Kilmaluag formation, and the horizon is independently dated as late Bathonian by ostracods (J. Athersuch pers. comm. 1988).

MORPHOLOGY, TAXONOMY AND EVOLUTION

The taxonomy of fossil conchostracans is mainly based on the characteristics of their carapace and minute ornamentation of growth bands, because their soft bodies and appendages are seldom preserved in fossils (but see Zhang *et al.* 1987, for Jurassic soft-part preservation). The distinctive leaids aside, many forms lack remarkable differences in shape of the carapaces, although some may have exceptional features of the umbo or dorsal margin (such as large umbo, umbonal node, reflected curved growth lines near dorsal margin). In most Jurassic and Cretaceous forms, the carapaces vary only from elliptical, oval, or subquadrate to subcircular, and their umbones are generally placed between the middle point and the anterior end of the dorsal margin, so the taxonomy is only dependent upon the variety of ornamentation. Sometimes, the evolution of ornamentation is very rapid and distinct in a particular basin or in a limited area belonging to the same river system. The non-marine Cretaceous of NE China has been successfully subdivided in this way (Zhang *et al.* 1976, pp. 44–45, 82–85, text-fig. 39; Chen and Shen, 1985, pp. 20–22, text-fig. 11). Thus we disagree with the low taxonomic status assigned to interspace ornament by Tasch (1969).

The variously developed growth lines of conchostracan carapaces are formed from the junction of neighbouring growth bands (Novojilov 1954, p. 96, text-fig. 69; Chen and Shen 1985, pp. 13–14; text-figs 7 and 8). These structures are clearly shown in SEM photographs in the present paper (Pl. 2, figs 8, 10, 11; Pl. 3, figs 6 and 9; Pl. 9, figs 9–12; pl. 10, figs 3–8). A row of tubes is situated on the lower margin of each growth band (= growth line), corresponding with a row of rivets on the prolongation of the next growth band (Text-fig. 2). The basal holes of these tubes are exposed on the interior surface of growth bands (Pl. 3, fig. 6). These tubes in *Dendrostracus* have a cross-bar in between (Pl. 3, figs 4 and 8), but those of *Neopolygraptia* are shorter and without the cross-bar (Pl. 2, figs 8, 10, 11; Pl. 10, figs 3–8). For *Skyestheria*, appearing in a higher horizon of the Lealt Shale Formation, these tubes contract and connect with each other to form beading on the lower margin of the growth lines (Pl. 4, figs 6 and 9).



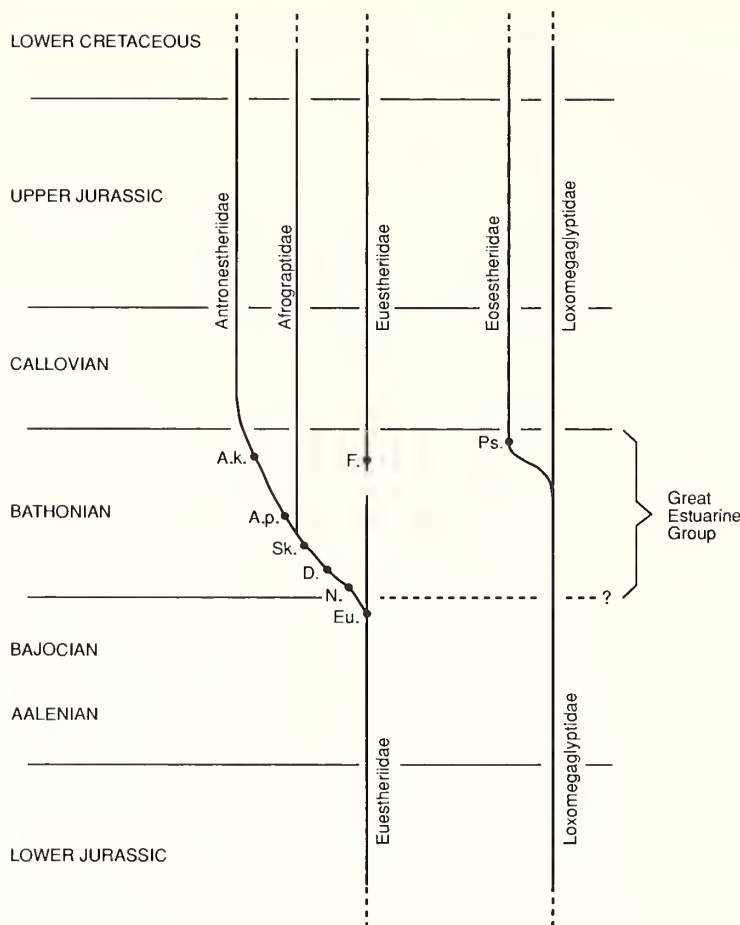
TEXT-FIG. 2. The construction of conchostracan growth bands and associated features.

Our morphological observations suggest some modifications to the classification of conchostracans given by Chen and Shen (1985) and to their evolutionary diagram (1985, p. 190, fig. 113). On the basis of the beading or serration along the lower margin of their growth lines, three genera erected herein (*Dendrostracus*, *Neopolygrapta* and *Skyestheria*) belong to the family Afrograptidae Novojilov, 1957. The origin of this family was regarded as uncertain by Chen and Shen (1985, p. 190, fig. 113). Our results suggest that these genera arose in the Middle Jurassic from members of the family Euestheriidae Defretin, 1965: *Dendrostracus* perhaps from *Euestheria* and *Neopolygrapta* from *Polygrapta*. The Afrograptidae (if monophyletic) thus originate in the Middle Jurassic and range into the lower Tertiary; they belong to the superfamily Eosestherioidea Zhang and Chen (*in* Zhang *et al.*, 1976) and there is no need for the superfamily Afrograptioidea Novojilov, 1957. According to interpretations in this paper, *Neopolygrapta* gave rise to *Skyestheria* in the Bathonian, and that in turn to the genus *Antronestheria* of the late Bathonian. *Antronestheria* is the type genus of the new family Antronestheriidae which includes other genera (see below) ranging from Middle Jurassic to Lower Cretaceous.

Pseudograpta Novojilov appears to be transitional between the families Loxomegaglyptidae and Eosestheriidae, a transaction already dated as middle Jurassic by Chen and Shen (1985, p. 190, fig. 113). However, our new material suggests that *Pseudograpta* should be included in the latter family rather than in the former as in Chen and Shen (1985, p. 109). *Pseudograpta* is not closely related to the group of genera belonging to the Euestheriidae or originating from that family within the Middle Jurassic, and its incoming near the top of the Great Estuarine Group is probably the result of immigration. It corresponds to a uniting of formerly distinct faunal provinces, as discussed below. Text-figure 3 summarizes our present views on evolutionary relationships.

PALAEOBIOGEOGRAPHY

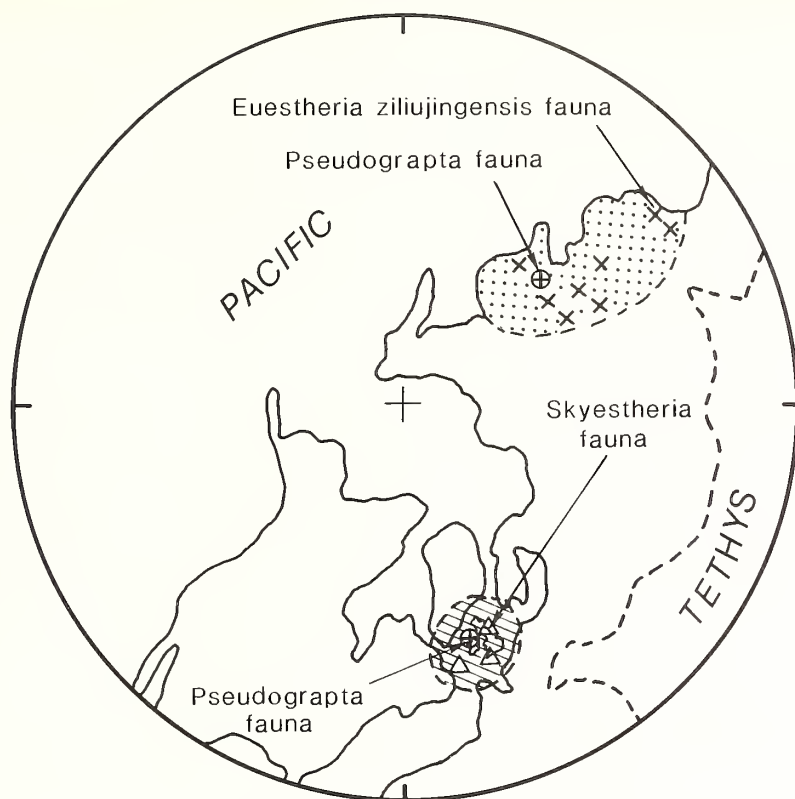
In this paper twelve conchostracan species in seven genera are described. Eight species in six genera (*Skyestheria*, *Dendrostracus*, *Neopolygrapta*, *Euestheria*, *Antronestheria* and *Fibrestheria*) form assemblages with overlapping stratigraphical ranges, belonging to or descended from the



TEXT-FIG. 3. Possible evolutionary relationships among some Jurassic conchostracan families (superfamily Eosestherioidea Zhang and Chen, 1976), as illustrated by genera occurring in the Great Estuarine Group. Based on Chen and Shen (1985, p. 120, fig. 113), as modified herein. Direct descent is not necessarily implied; see discussion in text. Eu., *Euestheria*; N., *Neopolygrapta*; D., *Dendrostracus*; Sk., *Skyestheria*; A.p., *Antronestheria praecursor*; A.k., *A. kilmaluagensis*; F., *Fibresteria*; Ps., *Pseudograptia*.

Euestheriidae. They are mostly new forms with very complex dendritic or cavernous ornamentation in their growth bands. This fauna is here named the *Skyestheria* Fauna, so far known mainly from Scotland, but with some of its members also recorded from England and from the Atlantic west of Ireland. It occurs stratigraphically below a fauna containing four species of *Pseudograptia*.

The *Euestheria ziliujingensis* fauna is widely distributed in the Middle Jurassic deposits from E Asia (Chen and Shen 1982). Apart from the index species, the fauna includes *A. haifanggonensis* Chen, *E. yanjiawanensis* Chen, *E. complanata* Chen, *E. rotunda* Chen, *E. jingyuanensis* Chen, and *Paleoptestheria chinensis* Chen. Their carapaces are generally small, elliptical or subcircular in outline, with simple small punctae or fine reticulate ornamentation of growth bands. *P. chinensis* from the Upper Shaximiao Formation of the Sichuan basin of SW China is a late member of this fauna and its cavernous ornamentation is similar to that of *Antronestheria*, described herein from late Bathonian deposits of Western Europe.



TEXT-FIG. 4. Map showing separate distribution of the early Middle Jurassic *Euestheria ziliujingensis* and *Skyestheria* faunas, and wide distribution of the later Middle Jurassic *Pseudograptia* fauna between China and western Europe. Polar projection based on Smith and Briden 1977.

By the end of the Middle Jurassic, the distinctness of the above-mentioned two conchostracan paleobiogeographic Provinces in the Euro-Asian continent (Text-fig. 4) disappeared, and they were replaced by a united *Pseudograptia* fauna. In this genus carapaces are large in size, with coarse hexagonal ornamentation of growth bands and very stout and convex growth lines (growth ridges). *P. orbita* and *P. munchisoniae* have been found in the Tuchengzi Formation of W Liaoning, NE China, as well as in Scotland (Zhang *et al.* 1976).

The two occurrences provide a remarkable example of the range of facies that conchostracans can inhabit, and of their wide dispersal. The Scottish occurrences are in near-coastal lagoonal dolomites, the Liaoning ones in thin green mudstones intercalated in thick, mainly fluvial, red-beds. They probably represent temporary pools or abandoned channels in flood-plains. And few places could be more different now than the shores of the Isle of Muck in the windy Hebrides, and the semi-arid uplands of Liaoning where the authors have jointly collected these conchostracans.

SYSTEMATIC PALAEONTOLOGY

Order CONCHOSTRACA Sars, 1867

Superfamily EOESTHERIOIDEA Zhang and Chen, 1976 (*in* Zhang *et al.* 1976)

Family EUESTHERIIDAE Defretin, 1865

Genus EUESTHERIA Deperet and Mazeran, 1912

Type species. Estheria minuta (Zieten, 1833)

Euestheria trotternishensis sp. nov.

Plate 1, figs 1–6

Etymology. From Trotternish, the northernmost peninsula of the Isle of Skye, Scotland.

Holotype. A left valve (BMNH In 63723, Pl. 1, fig. 2) from 2.5 m above the base of the Kildonnan Member, Lealt Shale Formation at Lonfearn Cliff, Trotternish, Skye.

Occurrence. Limited to the basal part of the Kildonnan Member of their Lealt Shale Formation (early Bathonian) in Skye and Eigg, NW Scotland. *Euestheria* indet., possibly the same species, occurs also in the Cullaidh Shale Formation in Strathaird (LEIUG 108064–6), and *Euestheria?* in bed 5 of the Kildonnan Member in Trotternish (LEIUG 108069).

Additional material. Numerous specimens are from the same locality as the holotype, where *E. trotternishensis* ranges through at least 1 m of strata below the holotype horizon (BMNH In 63724, 5, LEIUG 108060–3, 108067, 108181). A few specimens are from bed 1 of the type section of the Kildonnan Member, Lealt Shale Formation, Eigg (SM J49383–7; LEIUG 108179, 80).

Diagnosis. This new species differs from *E. minuta* in possessing numerous flattened growth bands, and from *E. ziliujingensis* (Zhang *et al.* 1976) of the early Middle Jurassic in China in having a subquadrate carapace outline.

Description. All specimens are well preserved carapaces or external moulds. Carapace small, subquadrate in outline, 4.2–5.5 mm long 3.3–4.3 mm high; dorsal margin short, umbo projecting above its subcentral part; anterior and posterior margins relatively straight, ventral margin arched downward; 23–35 growth bands, flattened, and with many small punctae ornamenting the surface especially in lower parts of the growth bands (Pl. 1, figs 1, 5, 6) or appearing as small granules on the external mould (Pl. 1, figs 3 and 4).

Genus FIBRESTHERIA gen. nov.

Etymology. From the fibrous appearance of the growth bands.

Type species. Fibrestheria puncta sp. nov. from the Kilmaluag Formation of Skye.

Occurrence. Late Bathonian; NW Scotland and Central England.

Diagnosis. Carapace of moderate size, subcircular or elliptical in outline; growth bands flattened, ornamented by minute and crowded punctae which form vertical lines.

Discussion. Among all forms of the family Euestheriidae, *Tenuestheria* from the Upper Cretaceous is similar to this new genus in ornamentation, but differs in its thin carapace, few and broad growth bands, and especially in its punctate sculpture without vertical alignment.

EXPLANATION OF PLATE 1

Figs 1–6. *Euestheria trotternishensis* sp. nov., from the basal Kildonnan Member, Lealt Shale Formation, Lonfearn Cliff, Skye. 1, 3, 4, BMNH In 63724; 1, $\times 42$; 3, $\times 72$; 4, $\times 120$. 2, holotype, BMNH In 63723, $\times 7.7$. 5 and 6, BMNH In 63725; 5, $\times 180$; 6, $\times 600$.

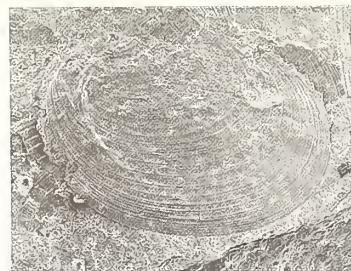
Figs 7–12. *Skyestheria elliptica* gen. et sp. nov., from the Lonfearn Member, Lealt Shale Formation, Rigg Burn, Skye. 7 and 8 holotype, BMNH In 63742; 7, $\times 12$; 8, $\times 180$. 9–11, BMNH In 63743; 9, $\times 42$; 10, $\times 120$; 11, $\times 180$. 12, BMNH In 63744, $\times 240$.



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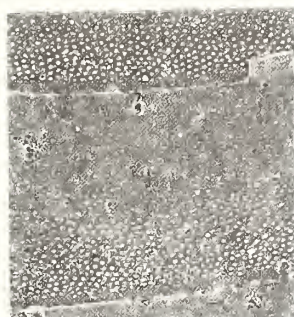
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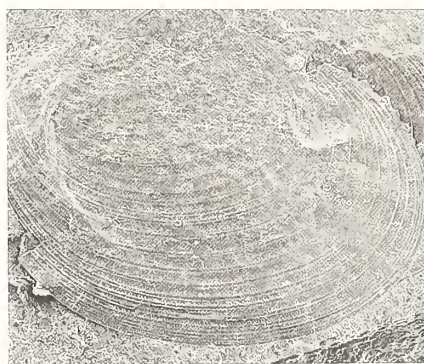
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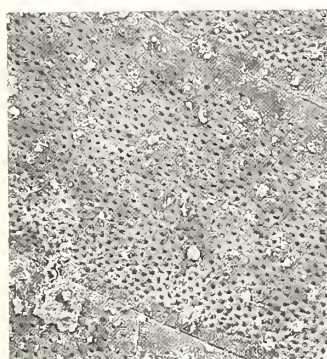
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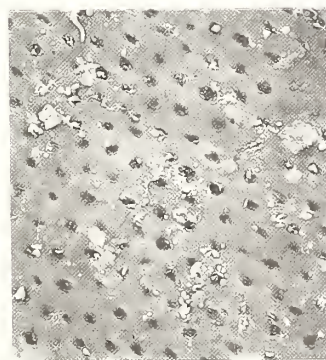
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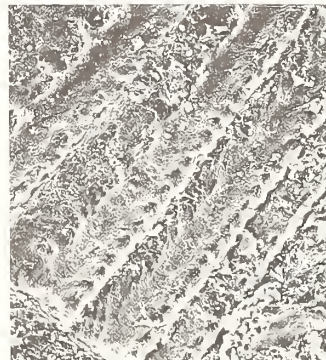
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Fibresteria puncta sp. nov.

Plate 4, figs 1, 8, 11

Etymology. From the punctate nature of the growth band sculpture.*Holotype.* An external mould of a right valve with some pieces of surviving shell (SM J49594–604I, Pl. 4, figs 1, 8, 11), from the Kilmaluag Formation of Skye.*Occurrence.* Kilmaluag Formation, Trotternish, Skye; so far known from one hand specimen only. *Fibresteria* cf. *puncta* occurs in the top 30 cm of the Blisworth Limestone (late Bajocian) on the M1 motorway near Newport Pagnell, Bucks (SP 8564 3840): BGS collection WA 908–910. This is probably within the *aspidioides* zone, late Bathonian (Cope *et al.* 1980, p. 39, fig. 6b).*Additional material.* Many individuals in the same slab (SM J49594–604) from Kilmaluag, Trotternish, Skye, bed 7 of Andrews (1985, p. 1122).*Diagnosis.* As for the genus.*Description.* Carapace of moderate size, elliptical to subcircular in outline, 8–11 mm long, 5–7 mm high; dorsal margin somewhat broken, umbo narrow and small, situated between its central and anterior end; anterior margin straight, posteroventral margin rounded; more than 30 growth bands with overlapping junctions, ornamented with minute and crowded punctae that are vertically aligned.

Family AFROGRAPTIDAE Novojilov, 1957

Genus NEOPOLYGRAPTA gen. nov.

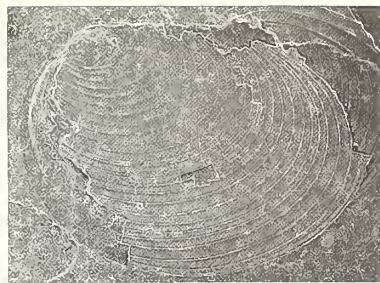
Etymology. This genus resembles *Polygrapta* Novojilov, 1957, but is younger.*Type species.* *Neopolygrapta lealtensis* sp. nov. from the Lealt Shale Formation and Cullaidh Shale Formation in Skye.*Occurrence.* Early Bathonian; NW Scotland.*Diagnosis.* Carapace small, elliptical or oval in outline; numerous growth bands with radial striae and cross bars, forming irregular reticulations with each other; growth lines with tubiform serrations of the lower margin.*Discussion.* The new genus and *Polygrapta*, distributed in the Euro-Asia continent during the Permian and Triassic, are much alike in ornamentation and growth bands, but the former differs from the latter in its tubiform serrations of the lower margin of the growth lines.*Neopolygrapta lealtensis* sp. nov.

Plate 2, figs 1–12; Plate 10, figs 1–12

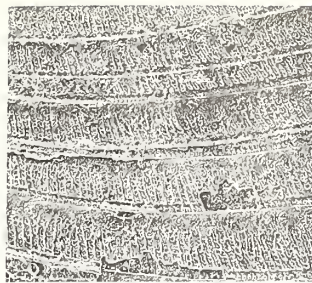
Etymology. From the Lealt River in Trotternish, Isle of Skye, Scotland.

EXPLANATION OF PLATE 2

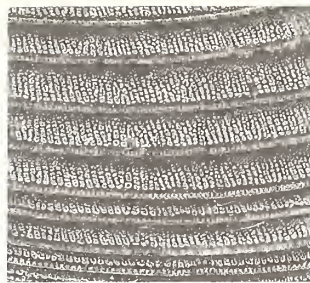
Figs 1–12. *Neopolygrapta lealtensis* gen. et sp. nov., from the Lealt Shale Formation of the Rudha nam Brathairean area, Skye; BMNH In 63728 and 63730 from the Lonfearn Member, BMNH In 63726, 7 from the Kildonnan Member. 1, holotype, BMNH In 63726, $\times 12$. 2 and 9, BMNH In 63727; 2, $\times 42$; 9, $\times 120$. 3–6, 12, external mould, BMNH In 63728; 3, $\times 42$; 4, $\times 12$; 5, $\times 90$; 6, $\times 90$; 12, $\times 420$. 7, BMNH In 63729, $\times 180$. 8, 10, 11, BMNH In 63730; 8, $\times 72$; 10, $\times 60$; 11, $\times 420$.



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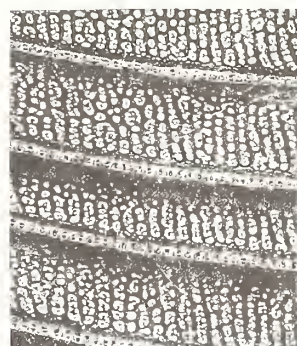
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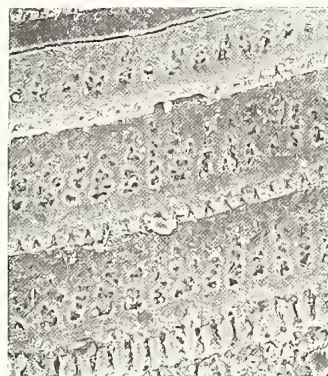
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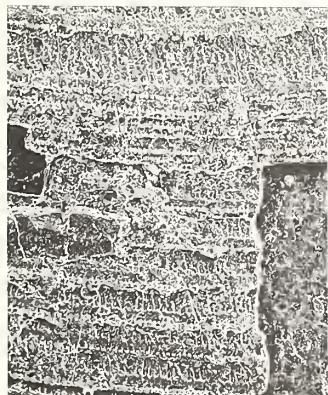
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Holotype. A left valve (BMNH In 63726, Pl. 2, fig. 1) from Upper Kildonnan Member of the Lealt Shale Formation, Lonfearn Cliff, Skye.

Occurrence. Kildonnan Member to lower Lonfearn Member of the Lealt Shale Formation, Isle of Skye.

Additional material. Many specimens from the Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Trotternish, Skye. Kildonnan Member: LEIUG 108082–4 from Rudha nam Braithairean; LEIUG 108085,6 from Lonfearn Cliff; LEIUG 108087–9 from South Rigg. Lonfearn Member: LEIUG 108070–81, 108184,5 from Rudha nam Braithairean; BMNH In 63728, LEIUG 108182,3 from Lonfearn Cliff; LEIUG 108194 from the Lealt River; LEIUG 108090,1, 108186–9 from North Rigg.

Diagnosis. As for the genus.

Description. Most specimens are well preserved carapaces or external moulds. Carapace small, oval or elliptical in outline, 4–5.5 mm long, 3–4 mm high; dorsal margin short and straight, umbo small, situated near its anterior end; anterior, posterior and ventral margins rounded; about 30 growth bands covered with radial striae and cross bars, striae simple and sometimes branching, cross bars fine and separating the interspace between striae into irregular reticulation; growth lines with short tubiform serrations of the lower margin. In external moulds of the carapace, growth bands with dotted ornamentation, radially arranged vertically, each dot consisting of several granules.

Genus DENDROSTRACUS gen. nov.

Etymology. From the dendritic appearance of the growth band sculpture.

Type species. *Dendrostracus hebridesensis* sp. nov. from the Lealt Shale Formation in the Isle of Skye.

Occurrence. Bathonian of Britain; the type species known only from the Great Estuarine Group of Scotland (see below).

Dendrostracus? also occurs in the Forest Marble, from 3–4 m beneath the Cornbrash, in the BGS Sandpool Farm borehole (SU 0122 9427) between Cirencester and Swindon. These strata most probably belong to the *aspidioides* zone, late Bathonian (Cope *et al.* 1980, p. 32).

Diagnosis. Carapace small, elliptical or oval in outline; growth bands flattened and ornamented by dendritic striae and small reticulations, reticulation separated by dendritic striae into many groups of meshwork patterns. Growth lines with tubiform serrated lower margins.

Discussion. This genus is similar in size and shape of carapace to *Neopolygrapta*, but differs from the latter in broader growth bands with dendritic ornament, and in the longer tubes forming the serrated lower margin of the growth lines, with a few cross bars between the tubes. The new genus is also somewhat similar in ornamentation of growth bands to *Jilinesstheria*, *Plectestheria* and *Glyptostracus* (Zhang *et al.* 1976, pl. 82, fig. 2; pl. 84, figs 5 and 6; pl. 133, figs 1–5) from the Upper Cretaceous of NE China, but differs from them chiefly in having a tubiform serrated lower margin to its growth lines. In addition, the dendritic striae of three Upper Cretaceous forms are much stronger and more thickened than these of *Dendrostracus*, and their reticulations between dendritic striae are of clearly different origin.

EXPLANATION OF PLATE 3

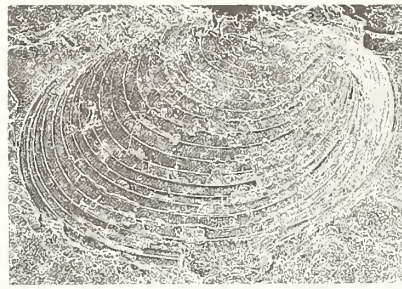
Figs 1–9. *Dendrostracus hebridesensis* gen. et sp. nov., from the Kildonnan Member, Lealt Shale Formation, south Rigg, Skye. 1 and 2 holotype, BMNH In 63731; 1, $\times 18$; 2, $\times 12$. 3 and 5, BMNH In 63732; 3, $\times 12$; 5, $\times 180$. 4 and 7, BMNH In 63732; 4, $\times 240$; 7, $\times 600$. 6, BMNH In 63733, $\times 120$. 8, BMNH In 63735, $\times 420$. 9, BMNH In 63736, $\times 200$.



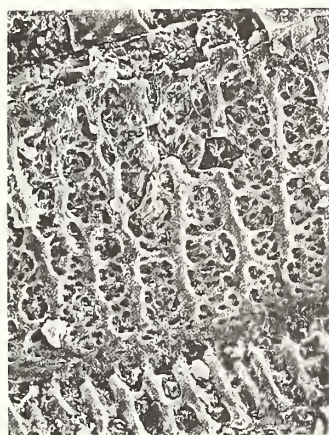
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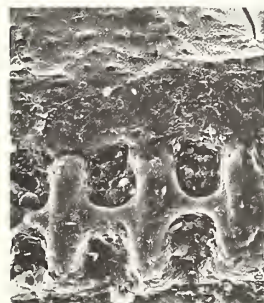
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Dendrostracus hebridesensis sp. nov.

Plate 3, figs 1–9; Plate 9, figs 9–12

Etymology. From the Hebrides, islands off NW Scotland.*Holotype.* An external mould of a left valve (BMNH In 63731, Pl. 3, fig. 2) from the Kildonnan Member, Lealt Shale Formation, in S Rigg, Skye.*Occurrence.* The species has a short recorded range in the upper Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Skye.*Additional material.* At least 21 specimens from the upper Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Trotternish, Skye. Kildonnan Member: LEIUG 108086, 108095–7 from Rudha nam Braithairean; LEIUG 108099, 100 from Lonfearn Cliff; BMNH In 63732–6, LEIUG 108098, 108190–3 from South Rigg, Lonfearn Member: LEIUG 108094 from Rudha nam Braithairean.*Diagnosis.* As for the genus.*Description:* Most specimens are poorly preserved internal or external moulds, but a few well preserved carapaces or external moulds show excellent ornamentation. Carapace small, oval or elliptic in outline, 3.5–4.6 mm long, 2.6–3.3 mm high; dorsal margin short and slightly arched upward; umbo small, situated subcentrally; anterior, posterior and ventral margins rounded, postventral margin obviously expanded; 15–30 growth bands, flattened and ornamented with dendritic striae and small reticulations which are separated by dendritic striae into many groups of mesh (each group generally including 6–8 meshes); occasionally only small reticulations in one or two growth bands near the ventral margin of carapace and without dendritic striae; a row of long tubiform structures attached to the lower margin of each growth line near the ventral side of the carapace, and a few cross bars between the tubes (Pl. 3, figs 4 and 8).

Genus SKYESTHERIA gen. nov.

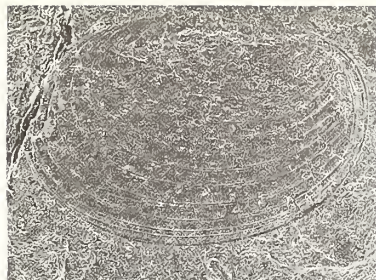
Etymology. From the Isle of Skye, Scotland.*Type species.* *Skyestheria intermedia* Chen and Hudson sp. nov. from the Lonfearn Member, Lealt Shale Formation in Skye.*Occurrence.* Bathonian, Isle of Skye.*Diagnosis.* Carapace small, oval, elliptical or subcircular in outline; numerous growth bands with *Neopolygrapta*-type ornamentation which crosses the whole band near the dorsal side of the carapace, but only occurs in the lower part of each band near the ventral side; growth lines with beaded lower margin.*Discussion.* This genus originates directly from *Neopolygrapta*. Its ornamentation of radial striae with cross bars shrinks back to the lower part of each growth band near the ventral side of the carapace and the upper part of the growth band is smooth. Along the lower margin of each growth

EXPLANATION OF PLATE 4

Figs 1, 8, 11. *Fibrestheria puncta* gen. et sp. nov., holotype, SM J49594-6041, from the Kilmaluag Formation, Kilmaluag, Skye. 1, $\times 5.5$. 8, $\times 42$. 11, $\times 414$.Figs 2, 3, 5, 6, 9, 12. *Skyestheria intermedia* gen. et sp. nov., from the Lonfearn Member, Lealt Shale Formation, Skye. 2, BMNH In 63738, $\times 12$. 3 and 5, holotype, BMNH In 63737; 3, $\times 72$; 5, $\times 12$. 6, BMNH In 63739, $\times 120$. 9, BMNH In 63740, $\times 420$. 12, BMNH In 63741, $\times 900$.Figs 4, 7, 10. *Antronestheria praecursor* gen. et sp. nov., from the upper part of the Lonfearn Member, Lealt Shale Formation, Lealt River, Skye. 4, holotype, SM J49409, $\times 4.8$. 7, BMNH In 63751, $\times 60$. 10, SM J49398, $\times 72$.



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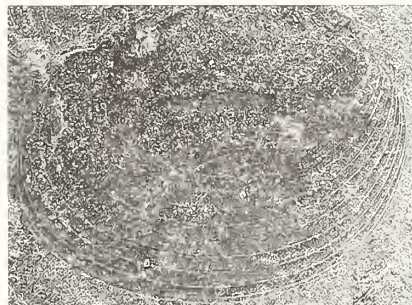
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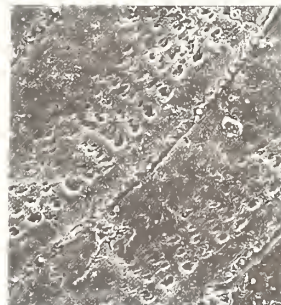
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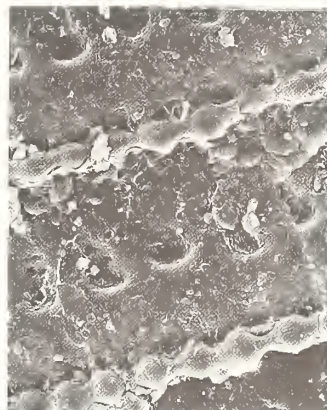
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line, the tubiform structure has been replaced by beading, presumably for consolidating the carapace, and the growth lines have thickened.

Skyestheria intermedia sp. nov.

Plate 4, figs 2, 3, 5, 6, 9, 12; Plate 9, figs 5–8

Etymology. This species is believed to occupy an intermediate position in the evolution of these conchostracans.

Holotype. An external mould of a left valve (BMNH In 63737, Pl. 4, figs 3 and 5) from the middle Lonfearn Member of the Lealt Shale Formation in the Lealt River, Skye.

Occurrence. Lonfearn Member of the Lealt Shale Formation in Skye.

Additional material. At least 32 specimens from the Lonfearn Member of the Lealt shale formation in Skye. BMNH In 63738, LEIUG 108104,5, 108198,9, from Rudha nam Braitharean; LEIUG 108112–4 from Lonfearn Cliff; BMNH In 63739, LEIUG 108102,3, 1081101,1, 108195–7 from Lealt River; BMNH In 63741, LEIUG 108106–9, 108200–5, from North Rigg; LEIUG 108115,6 from Elgol.

Diagnosis. *Skyestheria* with radial striae and cross bars in interspace sculpture of approximately equal strength.

Description. Carapace small, oval, elliptical or subcircular in outline, 3.5–4.5 mm long, 2.3–3.6 mm high; dorsal margin short and straight, umbo small and situated between its central and anterior end; anterior and ventral margins relatively straight, post-ventral margin rounded and slightly expanded; about 20–30 growth bands, ornamented by radial striae with cross bars through whole intervals in dorsal side, or only occupying the lower part of interval in ventral side; near ventral margin of carapace, thickened growth lines with beading along its lower margin and a row of shallow cavernous sculpture along its upper margin, several minute punctae surrounding the major structures in each case.

Skyestheria elliptica sp. nov.

Plate 1, figs 7–12

Etymology. From the shape of the carapace.

Holotype. A left carapace (BMNH In 63742, Pl. 1, figs 7, 8, 10) from the Lonfearn Member of the Lealt Shale Formation in Rigg Burn, Skye.

Occurrence. Lonfearn Member of the Lealt Shale Formation in Skye, from one bed only so far.

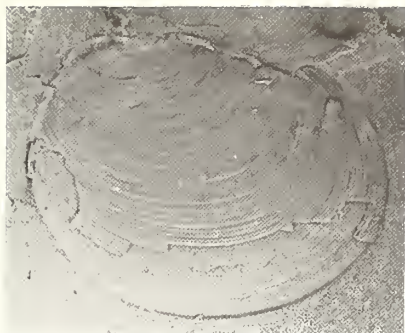
Additional material. Five specimens BMNH In 63743,4, LEIUG 108117,8, 108206 from same locality and same horizon as the holotype.

Diagnosis. *Skyestheria* with radial striae markedly stronger than cross bars in interspace sculpture.

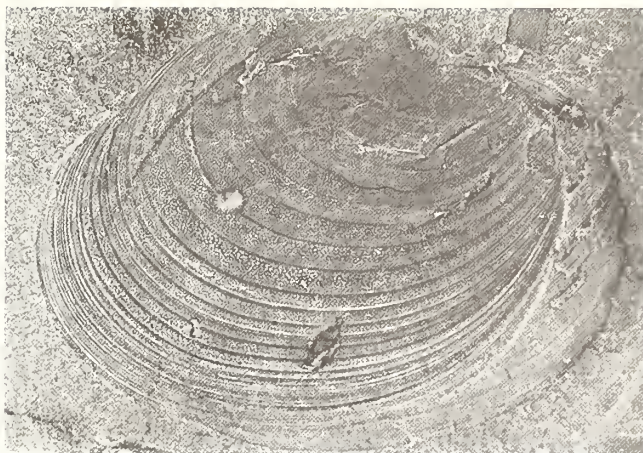
Description. This species is very similar in shape and size of carapace to *S. intermedia*, but differs chiefly in ornamentation. Its radial striae are consistently stronger and cross bars are weaker than those of *S. intermedia*: compare Plate 1, figures 9, 10, 11 with Plate 4, figure 6 and Plate 9, figures 5, 6, 7, 8. The carapace of the holotype is 3.2 mm long and 2.3 mm high. There are about 30 growth bands.

EXPLANATION OF PLATE 5

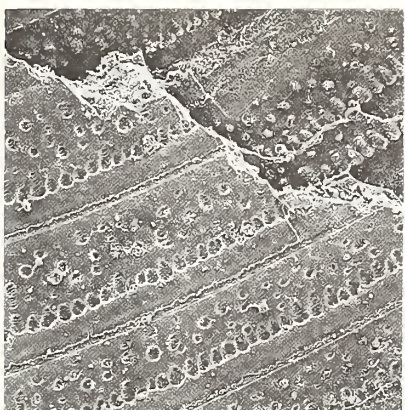
Figs 1–8. *Antronestheria kilmaluagensis* gen. et sp. nov., from the Kilmaluag Formation, Trotternish, Skye.
1, BMNH In 63746, $\times 9.6$. 2, holotype, BMNH In 63745, $\times 13.5$. 3–5 BMNH In 63747; 3, $\times 90$; 4, $\times 300$;
5, $\times 300$. 6, BMNH In 63748, $\times 600$. 7, BMNH In 63749, $\times 600$. 8, paratype, left valve BMNH 63750, $\times 20$.



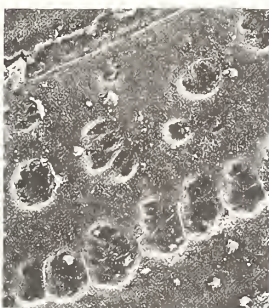
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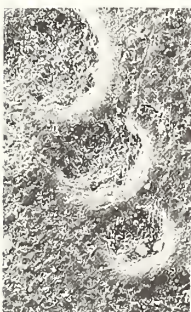
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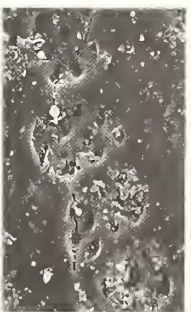
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Family ANTRONESTHERIIDAE nov.

Carapace elliptical or subcircular in outline; numerous growth bands with cavernous ornamentation; fossae of moderate or large size, simple or consisting of small punctae. Includes *Antronestheria* Chen and Hudson (gen. nov.), *Pseudestherites* Chen, 1976 (in Zhang *et al.* 1976), *Paleoleptestheria? chinensis* Chen, 1976 (in Zhang *et al.* 1976). Middle Jurassic to Lower Cretaceous.

Genus ANTRONESTHERIA gen. nov.

Etymology. From the Greek *antron*, a cave or cavity, in reference to the interspace sculpture.

Type species. *Antronestheria kilmaluagensis* sp. nov. from the Kilmaluag Formation (Bathonian) in NW Scotland and late Bathonian strata in the Porcupine Basin, NE Atlantic off Ireland.

Occurrence. Middle to upper Bathonian; NW Scotland, eastern England and Porcupine Basin off Ireland.

Diagnosis. Carapace moderate in size, oval to subcircular in outline; growth bands broad and flattened, with large cavernous ornamentation; fossae, consisting of several punctae, deepened and crowded along upper margin of each growth line; growth lines smooth and thickened.

Discussion. The new genus resembles *Paleoleptestheria chinensis* from the late middle Jurassic of SW China, and *Pseudestherites* from early Lower Cretaceous of NE China (Zhang *et al.* 1976, pl. 34, figs 1–8; pl. 39, figs 1, 2, 7, 8) in cavernous ornamentation, but differs from them in possessing several punctae in each fossa, and a row of crowded and deepened fossae along the growth line. *Antronestheria* probably evolved from *Skyestheria* of the Lonsfearn Member, but the latter differs from the former in having the beading along lower margin of each growth line and radial striae with cross bars in between.

Antronestheria kilmaluagensis sp. nov.

Plate 5, figs 1–8; Plate 9, figs 1–4

Etymology. From Kilmaluag, a village in north Trotternish, Isle of Skye, Scotland.

Holotype. An external mould of a left valve (BMNH In 63745, Pl. 5, fig. 2) from the Kilmaluag Formation in Kilmaluag Bay, Skye.

Occurrence. Commonly in the Kilmaluag Formation in Skye, NW Scotland; also in the same formation, Eigg (beds 1–9 of Andrews, 1985, p. 1125; LEIUG 108144–6). One recorded occurrence each from the Duntulm Formation, Lon Ostatoine, Skye, and the top of the Valtos Formation, Muck (LEIUG 108142–3). Also recorded from the late Bathonian, Porcupine Basin, and from the Blisworth Clay of the BGS Nettleton Bottom borehole, Lincolnshire (BGS BLJ 7762).

Additional material. At least 28 specimens from the Kilmaluag Formation, Trotternish, Skye. From Beds 1–7 of Andrews (1985, p. 1122) in Kilmaluag Bay: BMNH In 63746, LEIUG 108207–10, 108119–32. LEIUG 108133 from Lub Score. BMNH In 63747–50, LEIUG 108211–4 from Lon Sgapail.

EXPLANATION OF PLATE 6

Figs 1, 3, 5, 6b, 8. *Pseudograptia orbita* Chen, 1976, from the Kilmaluag Formation(?) near Monkstadt, Trotternish, Skye. 1 and 8, left valve, BGS, GSC 7296c; 1, $\times 6$; 8, $\times 22$. 3, 5, 6b, right valve, BGS, GSC 7296b; 3, $\times 6$; 5, $\times 22$; 6b, $\times 24$.

Figs 2, 4, 6a, 7. *Pseudograptia murchisoniae* (Jones, 1863), from the Kilmaluag Formation(?), near Monkstadt, Trotternish, Skye. 2 and 6a, lectotype, BGS, GSC 7296a; 2, $\times 6$; 6a, $\times 24$. 4, BGS, GSC 7296e, $\times 22$. 7, BGS, GSC 7296f, $\times 22$.

Fig. 6d. *Pseudograptia jonesi* sp. nov., BGS, GSC 7296d, from the Kilmaluag Formation (?), near Monkstadt, Trotternish, Skye, $\times 24$.



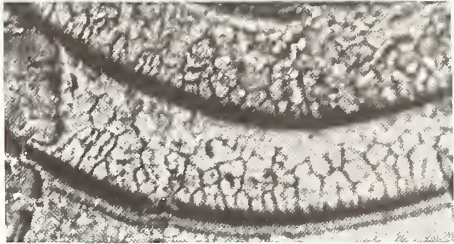
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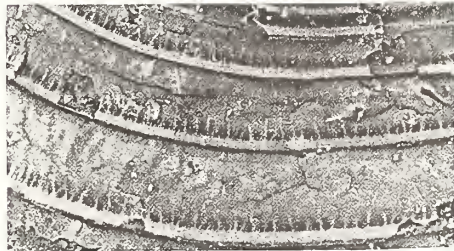
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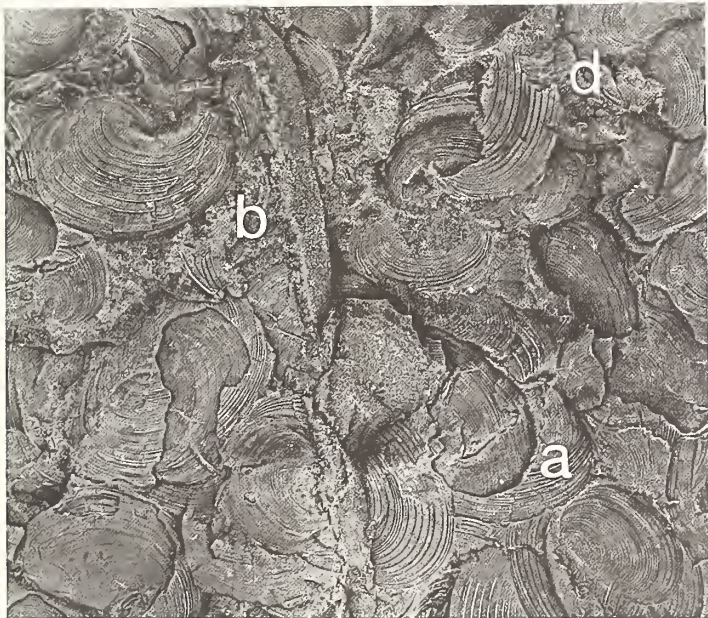
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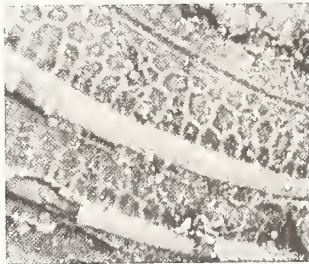
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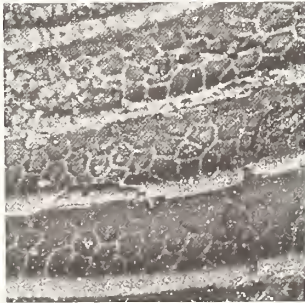
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Diagnosis. *Antronestheria* with large fossae in growth bands that are not aligned.

Description. Specimens are well preserved carapaces or external moulds. Carapace of moderate size, subcircular in outline, 3.8–8 mm long, 3–6 mm high; dorsal margin short, small umbo located near its centre; anterior and posterior margins relatively straight, postero-ventral margin rounded and slightly expanded; about 30 growth bands on carapace of adult, ornamented by cavernous sculpture; fossae subcircular or irregular-elliptical; each big fossa including several small punctae (Pl. 5, figs 4, 6, 7); a row of crowded and deepened fossae along upper margin of each growth line (Pl. 5, fig. 3); growth lines smooth and thickened, without beading or tubiform serrated lower margin. In external moulds, fossae appear as large pits which contain small granules (Pl. 5, fig. 5).

Antronestheria praecursor sp. nov.

Plate 4, figs 4, 7, 10

Etymology. This species is a precursor of the type species stratigraphically.

Holotype. An external mould of a right valve (SM J49409, Pl. 4, fig. 4) from upper Lonfearn Member of the Lealt Shale Formation in Lealt River, Isle of Skye.

Occurrence. Upper Lonfearn Member of the Lealt Shale Formation, Skye.

Additional material. Specimens are poorly preserved carapaces or exterior moulds (SM J49397–49414 (this series includes the holotype), BMNH In 693751, LEIUG 108136, 108215.6) from the upper Lonfearn Member of Skye.

Diagnosis. *Antronostheria* with fossae in growth bands aligned in vertical rows.

Description. Carapace subcircular in outline, 6.5–8 mm long, 4.75–5.9 mm high; anterior, posterior, and ventral margins all rounded; dorsal and umbonal area always poorly preserved, so growth lines not counted exactly; growth bands broad and flattened, covered with cavernous ornamentation; fossae vertically extended, crowded and deepened along upper margin of each growth line; growth lines thickened, without beading in their lower margins.

Remarks. *Antronestheria kilmaluagensis* is the dominant conchostracan of the upper Great Estuarine Group (see above), and *A. praecursor* from the upper part of the Lonfearn Member could be the earliest species of the genus.

Family EOSESTERIIDAE Zhang and Chen, 1976 (*in* Zhang *et al.* 1976)

Genus PSEUDOGRAPTA Novojilov, 1954

Type species. *Estheria munchisoniae* (Jones, 1863), from Upper Kilmaluag Formation (?) in Skye and Muck, NW Scotland.

Occurrence. Late Middle Jurassic; W Europe and E Asia.

EXPLANATION OF PLATE 7

Figs 1, 4, 5, 7. *Pseudograptia jonesi* sp. nov. 1, holotype, BGS, GSC 7296g, from the Kilmaluag Formation(?), Skye (associated with lectotype of *P. munchisoniae*), $\times 6$; 4 and 5, BGS, GSC 7296h, fragments of same shell; 4, $\times 96$; 5, $\times 42$. 7, BMNH In 63752, from the Upper Kilmaluag Formation, Camas Mor, Muck, $\times 43$.
Fig. 2. *Pseudograptia orbita* Chen, 1976, from the Upper Kilmaluag Formation, Camas Mor, Muck, BMNH In 63754, $\times 5.6$.
Figs 3, 6, 8–10. *Pseudograptia munchisoniae* (Jones, 1863), from the Upper Kilmaluag Formation, Camas Mor, Muck. 3 and 6, BMNH In 63753; 3, $\times 5.6$; 6, $\times 6$. 8–10, BMNH In 63755–7, respectively; 8, $\times 420$, 9, $\times 420$, 10, $\times 42$.



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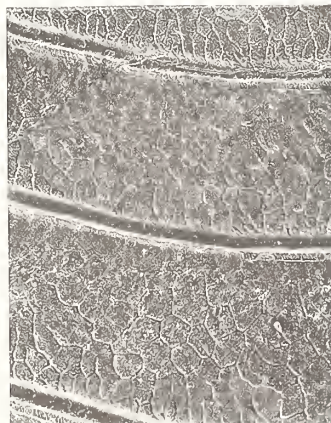
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Diagnosis. Carapace large, elliptical or subcircular in outline; growth bands broad and flattened, ornamented by bold polygonal reticulations in dorsal and central parts of carapace, and radial striae in ventral or postero-ventral parts; growth lines stout and convex (growth ridges), without beading or tubiform marginal structures.

Discussion. This genus is similar in ornament to *Eosestheria*, but differs in its stout and convex growth ridges and in the coarser polygonal reticulations of its growth bands. In general, the change from reticulation near the dorsal side into radial striae near the ventral side is abrupt for *Pseudograptia* (except *P. morrissi* sp. nov.), but for *Eosestheria* there is a transitional area of two types of ornament in the carapace. This genus has a strong resemblance to *Nestoria* in stout and convex growth ridges and bold polygonal reticulation, but the latter differs from the former in not having radial striae on its growth bands near the ventral margin of the carapace. Novojilov (1954, pp. 81–82, pl. 15, fig. 10; pl. 16, fig. 1) referred another three species to this genus: *P. andrewsi* (Jones), *P. orientalis* (Eichwald), and *P. olonchurenensis* Novojilov, but unfortunately so far no bold polygonal reticulations or stout convex growth ridges are to be found among them.

Pseudograptia murchisoniae (Jones, 1863)

Plate 6, figs 2, 4, 6a, 7; Plate 7, figs 3, 6, 8–10

- 1863 *Estheria murchisoniae* Jones, pp. 100–101, pl. 3, figs 1–12.
- 1946 *Bairdestheria murchisoniae* (Jones); Raymond, p. 227.
- 1954 *Pseudograptia murchisoniae* (Jones); Novojilov, p. 81.
- 1976 *Pseudograptia* aff. *murchisoniae* (Jones); Zhang *et al.*, p. 173, pl. 56, figs 1–8.

Lectotype. An external mould of a left valve from the syntype (British Geological Survey, Geological Society Collection (BGS, GSC) 7296a, Pl. 6, figs 2 and 6a) figured by Jones in 1863 (pl. 3, fig. 2) from the Upper Kilmaluag Formation (?) in the canal, Icolmkill, Skye.

Occurrence. Upper Kilmaluag Formation (?) from 'Icolmkill', Skye and Camas Mor, Muck, NW Scotland.

Material. Eleven specimens: syntype (BSG, GSC 7296) from Skye; BMNH In 63753, 63755–7, LEIUG 108137–41, 108217 from Camas Mor, Muck. Muck specimens from Beds 13 and 15 of the Kilmaluag Formation (Andrews 1985 p. 1125).

Original Description. This species was described by Jones (1863 p. 100) as follows: 'carapace-valve nearly elliptical, the straight hinge-line interfering with the symmetry of the outline. The umbo is forward, at the end of the hinge-line, and scarcely affects the outline. The anterior extremity has a flatter curve than the posterior. About eighteen delicate concentric ridges are usually distinctly to be observed, with their rather wide interspaces; but some carapaces have nearly thirty ridges, with very narrow interspaces. The ornament of the interspaces is essentially a bold, irregularly hexagonal reticulation, like that of *E. minuta*; but it generally takes on a distinct, short, vertical wrinkling of the lower part of the interspace. This sometimes presents the modification seen in figs 3 and 8, where the wrinkling is of a much smaller pattern, and reached half way up, or all across the interspace. Sometimes a delicate, horizontal wrinkling, without hiding altogether the reticulate structure of the shell. Not infrequently, both the broad and the narrow interspaces are blank (figs 6 and 10).' Judging from this description, and new observations on the slab bearing Jones's syntype specimens, there are at least three different forms: the first form is elliptical in outline of carapace, with 16–32 growth bands ornamented by bold irregular hexagons near dorsal side and radial striae near ventral side; the second form is subcircular in outline, with 15–20 growth bands and ornamentation as the first; the third form is also

EXPLANATION OF PLATE 8

Figs 1–9. *Pseudograptia morrissi* sp. nov., from the Upper Kilmaluag Formation, Camas Mor, Muck. 1, BMNH In 63758, $\times 8.4$. 2, holotype, BMNH In 63759, $\times 8$. 3, BMNH In 63760, $\times 5$. 4–9, BMNH In 63751; 4, $\times 24$; 5, $\times 12$; 6, $\times 24$; 7, $\times 60$; 8, $\times 240$; 9, $\times 420$.



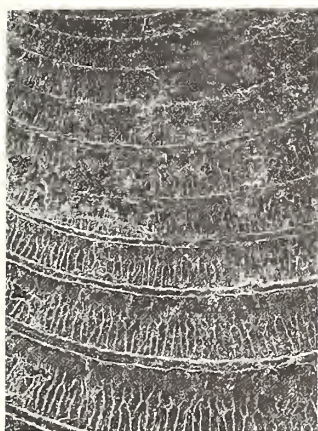
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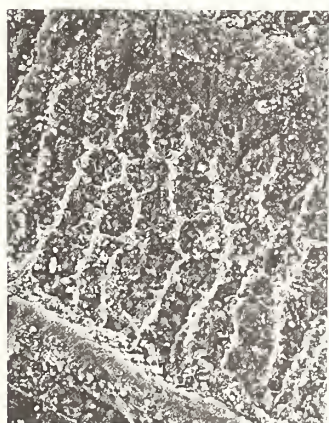
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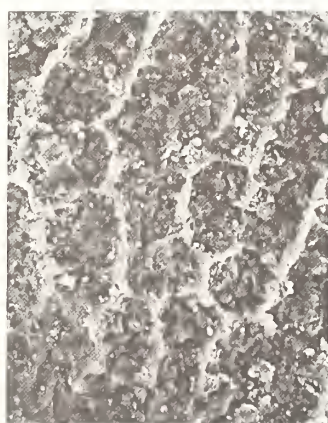
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elliptical in outline, but with about 40 narrow growth bands, ornamented mostly by short radial striae. The present authors consider that this famous conchostracan species should be represented by the first elliptical form, and assign an exterior mould of left carapace from Jones's slab (Pl. 6, figs 2 and 6a) as the lectotype. The second form is referred to *P. orbita* Chen, and the third described herein as *P. jonesi* sp. nov. (see below).

Revised description. Carapace large, elliptical in outline, 7.5–10.3 mm long, 5–6.2 mm high; dorsal margin long and straight, umbo small and subanterior; anterior margin straight, the posterior rounded, the ventral arched downward; broad growth bands ornamented by bold polygonal reticulations, mesh mostly irregular hexagonal, mesh wall thin, mesh base shallow and flattened with short septum-like structure (Pl. 7, fig. 9); radial striae frequently developed in the lower part of each growth band near ventral side of carapace; growth ridges stout and smooth.

Remarks. Novojilov (1954, pl. 11, fig. 2; pl. 15, figs 5–9) described some specimens from the Upper Jurassic in Mongolia, referring them to this species, but they may belong to *Eosestheria* according to their ornament.

Pseudograptia orbita Chen, 1976 (in Zhang *et al.* 1976)

Plate 6, figs 1, 3, 5, 6b, 8; Plate 7, fig. 2

1976 *Pseudograptia orbita* Chen; Zhang *et al.* pp. 173–174, pl. 55, figs 1 and 2.

Holotype. An exterior mould of a left carapace from the Middle Jurassic Tuchengzi Formation at Cajiagou near Jinlingsi, W Liaoning, China.

Occurrence. Upper Kilmaluag Formation (?) in 'Icolmkill', Skye and Camas Mor, Muck.

Additional material. A right valve and another left valve from the same slab as *P. munchisoniae* (BGS, GSC 7296b, c), Skye; five specimens BMNH In 63754, 63762, LEIUG 108139 (two specimens), LEIUG 108141 (M88-CPJ2) from the Upper Kilmaluag Formation at Camas Mor, Muck.

Description. Carapace large, subcircular in outline; 8.5–12 mm long, 6.5–8.5 mm high; dorsal margin short, small umbo located between its centre and anterior end; anterior, posterior and ventral margins rather rounded, postero-ventral margin slight expanded; growth ridges stout and convex; 16–32 growth bands broad and flattened, ornamented with bold irregular hexagons in dorsal and middle parts of carapace, and short radial striae in ventral part.

Remarks. This species is frequently associated with *P. munchisoniae* and it is very similar to the latter in ornamentation, but differs in outline of carapace. They might be sexual dimorphs, but so far there is no evidence of appendages or eggs in the fossils.

Pseudograptia jonesi sp. nov.

Plate 6, fig. 6d; Plate 7, figs 1, 4, 5, 7

Etymology. In honour of Professor T. R. Jones, author of the first monograph on fossil conchostracans.

EXPLANATION OF PLATE 9

Figs 1–4. *Antronestheria kilmaluagensis* gen. et sp. nov., BMNH In 63747, Kilmaluag Formation, Trotternish, Skye. Stereo pairs. 1 and 2, $\times 90$. 3 and 4, $\times 180$.

Figs 5–8. *Skyestheria intermedia* gen. et sp. nov., BMNH In 63739 Lonfearn Member, Lealt Shale Formation, Lealt River, Skye. Stereo pairs. 5 and 6, $\times 90$. 7 and 8, $\times 180$.

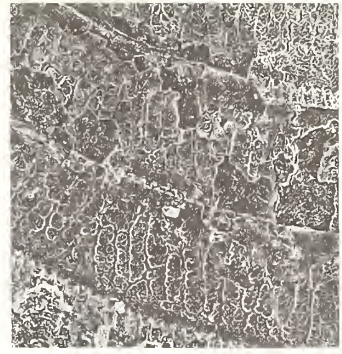
Figs 9–12. *Dendrostracus hebridesensis* gen. et sp. nov., BMNH In 63733, Kildonnan Member, Lealt Shale Formation, south Rigg, Skye. Stereo pairs. 9 and 10, $\times 90$. 11 and 12, $\times 180$.



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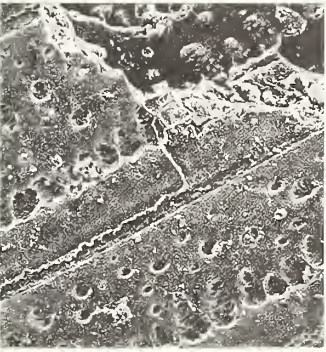
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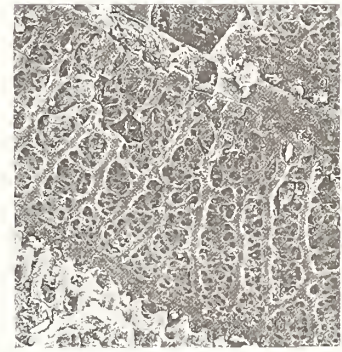
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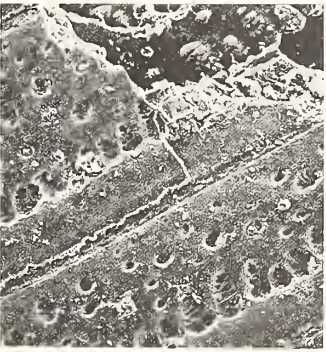
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Holotype. An external mould of a right valve with a few pieces of surviving 'chitinous' shell in lower surface of the syntype slab (BGS, GSC 7296g, Pl. 7, fig. 1), from the Upper Kilmaluag Formation (?) at Icolmkill, Isle of Skye; fragments from the same shell showing ornament (BGS, GSC 7296h, Pl. 7, figs 4 and 5).

Occurrence. Upper Kilmaluag Formation (?); 'Icolmkill', Skye and Camas Mor, Muck.

Additional material. Apart from the holotype, there are two specimens: one from the slab's upper surface (BGS, GSC 7296d, Pl. 6, fig. 6), another (BMNH In 63752) from upper Kilmaluag Formation at Camas Mor, Muck (bed 15 of Andrews 1985).

Diagnosis. *Pseudograptia* with narrow and numerous growth bands, and dominant short radial striae on the growth bands.

Description. Carapace moderate to large, elliptical in outline, 7.7–11 mm long, 4.7–7.5 mm high; dorsal margin poorly preserved, umbo situated subcentrally or near its anterior end; anterior and posterior margins somewhat straight, ventral margin broadly arched downward; narrow growth bands about 40 in number, ornamented with short radial striae in lower part of each interval, and reticulation only in dorsal region of carapace; growth ridges stout and smooth.

Pseudograptia morrisi sp. nov.

Plate 8, figs 1–9

Etymology. For Mr S. Morris of the Natural History Museum, London, who collected these conchostracans with us in August 1988.

Holotype. An external mould of a left valve (BMNH In 63759, Pl. 8, fig. 2) from the Upper Kilmaluag Formation at Camas Mor, Muck.

Occurrence. Upper Kilmaluag Formation, Camas Mor, Muck.

Additional material. Six specimens (BMNH In 63758, 63760, 1; LEIUG 108218–20); locality and horizon same as holotype (beds 13–15 of Andrews 1985).

Diagnosis. Small *Pseudograptia* with reticulation in dorsal growth bands passing into radial striae in ventral growth bands.

Description. Most specimens are poorly preserved internal or external moulds, and only a few with 'chitinous' shell and ornamentation on growth bands. Carapace of moderate size, elliptical in outline, 5.4–9.8 mm long, 3.8–6.5 mm high; dorsal margin straight and long, small and narrow umbo situated near its anterior end; anterior and posterior margins curved symmetrically, ventral margin arched broadly and downward; growth lines thickened; 15–21 growth bands, broad and flattened, ornamented by very irregular polygons near dorsal side and gradually changed into striae near ventral or postero-ventral parts of carapace.

Discussion. This species is the smallest of the genus *Pseudograptia*, and might be referred to *Eosestheria* based on the transitional ornament from reticulation in the dorsal side to radial striae in the ventral side, but for the thickened growth lines. *Eosestheria* was widely distributed in E Asia during the late Jurassic and it was considered to evolve from *Nestoria* (Zhang *et al.* 1976, pp. 79–80,

EXPLANATION OF PLATE 10

Figs 1–12. *Neopolygrapta lealtensis* gen. et sp. nov., Lealt Shale Formation, Lonfearn, Skye. Stereo pairs. 1, 2, 9–12, BMNH In 63728; 1 and 2, $\times 90$; 9 and 10, $\times 90$; 11 and 12, $\times 180$. 3–8, BMNH In 63730; 3 and 4, $\times 180$; 5 and 6, $\times 90$; 7 and 8, $\times 180$.



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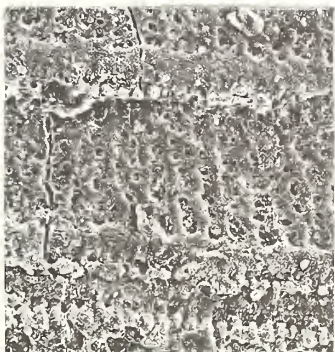
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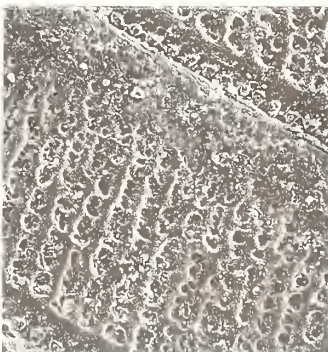
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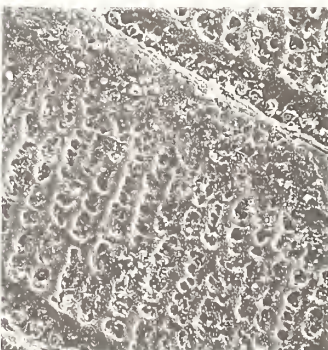
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text-fig. 38). Based on the new material from the Isle of Muck, there is a greater possibility that *Pseudograptia morrisi* sp. nov. is the ancestor of *Eosestheria*.

Acknowledgements. We thank the Royal Society and Academia Sinica for sponsoring Chen Pei-ji's visit to Leicester and J. D. Hudson's visit to China, and the British Petroleum Company plc for further support for Chen Pei-ji, as well as allowing us to examine material from their Porcupine Basin cores. We thank Sam Morris, Matthew Wakefield and Mark Wilkinson for help in the field, and Sam Morris, Roy Clements, Mike Dorling and Hugh Ivimey-Cook for access to material in their charge at the British Museum (Natural History), Leicester University, the Sedgwick Museum, Cambridge, and the British Geological Survey respectively, and for discussing it with us. Rod Branson operated the SEM and Sue Button drew the figures. Clare Stanga, Liane Baldock and Christine Burnett processed several versions of the manuscript.

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A NEW PRIMITIVE DINOCEPHALIAN MAMMAL-LIKE REPTILE FROM THE PERMIAN OF SOUTHERN AFRICA

by BRUCE S. RUBIDGE

ABSTRACT. A new genus of tapinocephalinc dinocephalian, *Tapinocaninus pamela*, is described from the lowermost biozone of the Beaufort Group in South Africa. *Tapinocaninus* is older than any dinocephalian previously discovered in Africa, being early Late Permian (Ufimian–Kazanian) in age. It is considered to belong to the subfamily Tapinocephalinae but retains plesiomorphic features which are absent in the Tapinocephalinae and were previously considered characteristic of the more primitive Titanosuchinae. The Titanosuchinae are distinguished from the Tapinocephalinae in the form of the postcanine teeth (leaf-shaped and serrated in the former and bearing a lingual heel in the latter) and in the pachyostotic thickening of the skull roof of the latter.

DINOCEPHALIANS were a group of medium to large mammal-like-reptiles which included the largest land-living animals to have existed up to Late Permian (Ufimian–Kazanian) times. They were present among the earliest therapsid fauna of the San Angelo Formation of Texas (Olson 1962) and the Russian Ocher Formation (Tchudinov 1983), and also formed an important part of the therapsid fauna of the *Tapinocephalus* Zone (Dinocephalian Assemblage Zone) of the Beaufort Group in South Africa (Boonstra 1969, 1971; Kitching 1977; Keyser and Smith 1978).

The Dinocephalia are the earliest group of therapsids for which a significant adaptive radiation can be identified (Ruben 1986), but for all their early success, they became completely extinct by the close of *Tapinocephalus* Zone (Dinocephalian Assemblage Zone) times, leaving no descendant groups (Boonstra 1971; Kemp 1982). The infra-order Dinocephalia was considered to consist of six families, namely Estemmenosuchidae, Brithopodidae, Anteosauridae, Titanosuchidae, Tapinocephalidae and Styraocephalidae (Boonstra 1963a; Kemp 1982). More recently, King (1988) reclassified these as subfamilies of the three families Estemmenosuchidae, Brithopodidae, and Titanosuchidae, and regarded *Styraocephalus*, the only genus in the family Styraocephalidae, as *incertae sedis*. Of the three families recognized by King, only the Estemmenosuchidae have not yet been found in Africa. The classification of King (1988) is used in this study. Apomorphic features which characterize the Dinocephalia as a distinct infraorder are the presence of intermeshing incisor teeth in the upper and lower jaws (Boonstra 1962, 1963a; Hopson and Barghusen 1986; King 1988), and incisor teeth with lingual heels (Hopson and Barghusen 1986).

MATERIALS AND METHODS

Five dinocephalian skulls, which are considered to belong to the same genus, have recently been collected in rocks of the Late Permian *Eodicynodon* Zone, a newly identified biozone at the base of the Beaufort Group (Rubidge 1987). All but one of these fossils were found on Modderdrift farm, three from the same sandstone outcrop in close proximity. These three specimens were found by Mr John Nyaphuli and are housed in the Karoo fossil reptile collection of the National Museum, Bloemfontein (specimens NMQR 2985, 2986, 2987), while the fourth specimen (ROZ K95), although found by the author, is housed in the private fossil collection of Mr Roy Oosthuizen on his farm, Zwartskraal, in the district of Prince Albert. The fifth specimen (NMQR 3097), which consists only of a skull roof and some isolated teeth, was found on Swartgrond farm in the Rietbron district and is now housed in the National Museum in Bloemfontein.

The lower jaws are preserved in all but one of the specimens, but those of ROZ K95 and NMQR 2986 were too firmly appressed to the skull prior to fossilization to prepare on the lingual side. Although the right ramus of the lower jaw of the specimen NMQR 2985 could be dissociated from the skull, the bones of the lower jaw on the medial side were damaged and disoriented prior to fossilization. By far the best preserved lower jaw is that of NMQR 2987 which is undistorted and still bears several teeth *in situ*.

All the skulls were prepared with the aid of air-driven engravers. A hammer and chisel and small angle grinder were used in areas where there was an excess of matrix covering the bone and where there was no chance of damage to the bone. Glyptal 1276 Lacquer Cement, supplied by General Electric, was used as an adhesive.

Institutional abbreviations are: NMQR, National Museum, Bloemfontein; ROZ K, Roy Oosthuizen Collection, Klaarstroom.

SYSTEMATIC PALAEOLOGY

Subclass SYNAPSIDA Osborn, 1903

Order THERAPSIDA Broom, 1905

Infraorder DINOCEPHALIA Seeley, 1894

Family TITANOSUCHIDAE Boonstra, 1972

Subfamily TAPINOCEPHALINAE Lydekker, 1890

Tapinocaninus gen. nov.

Type species. Tapinocaninus pamela sp. nov.

Diagnosis. Large tapinocephaline dinocephalian. Moderate pachyostosis with broad postorbital bar. Temporal opening relatively large for tapinocephaline, and hence relatively narrow intertemporal region. Premaxilla forming anterior and antero-lateral border of the internal nares. Maxilla with very short contact on lateral side of internal nares such that the palatine and premaxilla almost meet. Vomer narrow in ventral view. Heterodont dentition with medium-sized canine tooth lacking definite crushing heel in both upper and lower jaw. Lower canine passing in front of upper canine rather than on lingual side. Five larger incisor teeth in premaxilla, all with crushing heel. Quadrate condyles situated below posterior border of orbit. Several small palatal teeth on palatine boss.

Etymology. Greek *tapino*, humble; Latin *caninus*, canine. The name refers to the reduced size of the canine tooth relative to that of the Titanosuchinae and indicates that the genus belongs to the subfamily Tapinocephalinae.

Tapinocaninus pamela sp. nov.

Text-figures 1–3.

Diagnosis. As for genus.

Etymology. The species is named in honour of my mother Pam Rubidge who encouraged my interest in palaeontology and was with me in the field when this fossil was discovered.

Holotype. Specimen NMQR 2987. Skull and mandible. Left side of skull well preserved with several teeth; parietal and occipital regions on right side damaged as a result of weathering.

Paratypes. Specimens NMQR 2985 (skull and mandible), NMQR 2986 (skull and mandible), ROZ K95 (skull and mandible).

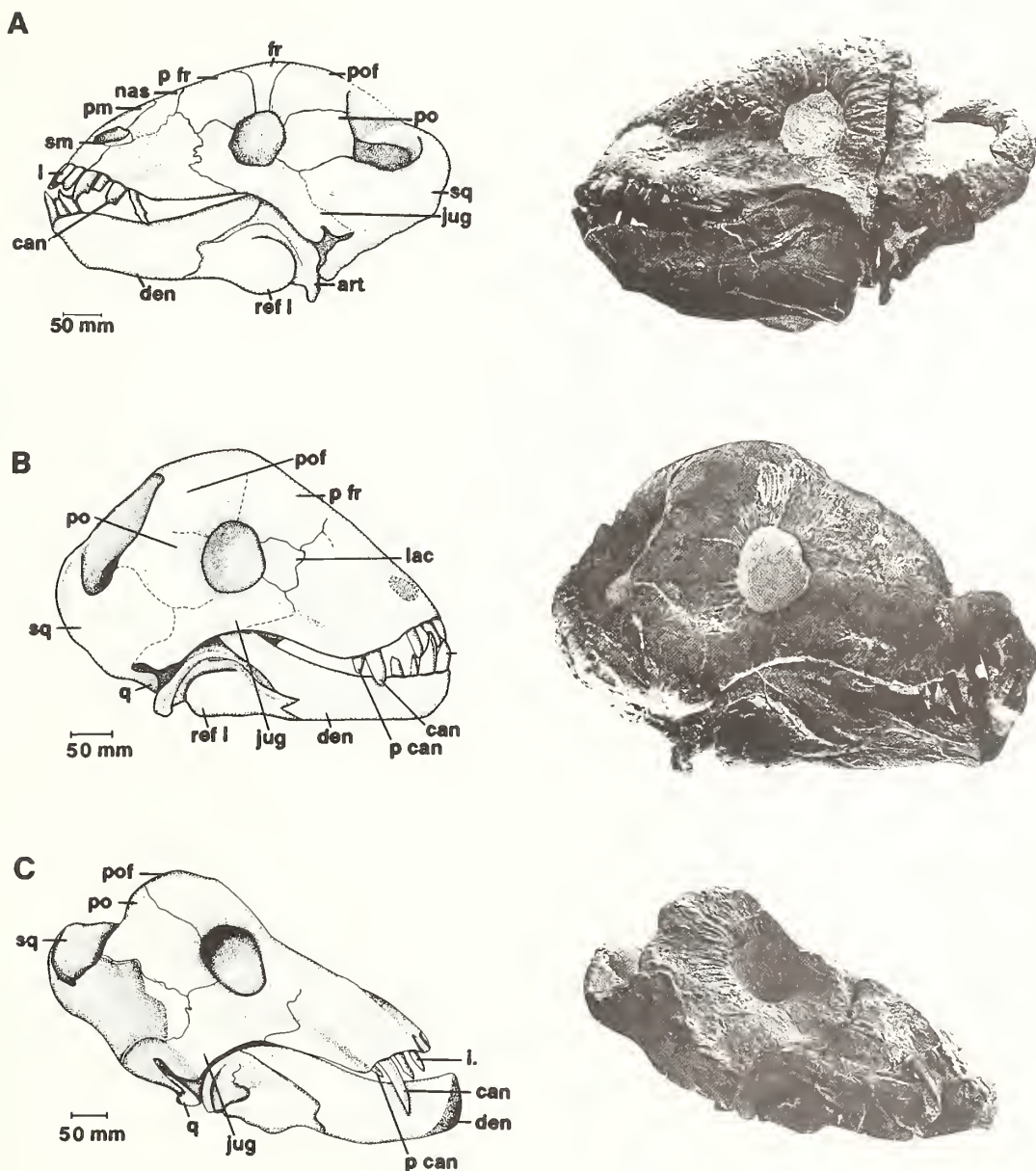
Type horizon and locality. *Eodicynodon* Zone (Rubidge 1987) at the base of the Beaufort Group (Ufimian–Kazanian age) on Modderdrift farm, Prince Albert, South Africa (map sheet: South Africa 1:50000, Sheet 3322 BA Seekoegat, first edition).

DESCRIPTION

Skull Roof

In their general shape the newly discovered dinocephalian skulls resemble those of other tapinocephaline dinocephalians in that the skull roof is greatly pachyostosed and the postorbital bar is extremely thick.

The anterior portion of the snout is formed by the *premaxilla* which also forms the anteroventral, anterior, and dorsal border of the external nares. The premaxilla extends posterodorsally as a narrow projection on the



TEXT-FIG. 1. *Tapinocanius pamela*, lateral view. A, NMQR 2987; B, NMQR 2986; C, ROZ K95.

roof of the snout to a point approximately halfway between the external nares and the orbit where it is in sutural contact with the nasals. The contact of the premaxilla with the maxilla on the lateral side of the snout is an obliquely orientated suture which extends ventrally from approximately one-third of the way along the antero-ventral side of the external nares to the front of the canine alveolus.

Anteriorly, the *nasal* is in contact with the posterior border of the external naris and the septomaxilla, while it is in contact with the maxilla on the antero-ventral side and the prefrontal on the postero-ventral side. On the dorsal side of the skull the nasals extend posteriorly as a narrow projection medial to the enlarged prefrontal bone and meet the frontals in line with the anterior limit of the orbits.

The *maxilla* forms the greater portion of the lateral surface of the snout. Dorsally it is in sutural contact with the nasal, and posteriorly with the prefrontal, lachrymal, and jugal in an almost straight vertical line anterior to the orbit. The lateral surface of the maxilla, above the alveolus of the canine, is swollen laterally to accommodate the root of the canine as in titanosuchine dinocephalians (Boonstra 1962).

As in all known South African dinocephalians, the *prefrontal* is a prominent bone and forms the antero-dorsal border of the orbit. Posteriorly and posterodorsally, the prefrontal is in contact with the frontal, antero-dorsally with the nasal and antero-ventrally with the maxilla. Almost halfway down the front of the orbit, the prefrontal is in sutural contact with the *lachrymal* which extends on the lateral side of the skull anterior to the orbit. The suture between the lachrymal and *jugal* is situated slightly less than one-third of the way up from the base of the orbit and slopes anteroventrally.

The *jugal* is a prominent bone which forms the ventral margin of the orbit and of the lateral side of the cranium in the suborbital region. It extends slightly anteroventrally of the orbit on the lateral surface of the snout and has a long sutural contact with the posterior edge of the maxilla. Behind this contact, the ventral margin of the skull curves posteroventrally until it reaches its most ventral point below the postorbital bar lateral to the articulatory condyles of the quadrate. From here, the ventral margin is notched posterodorsally so that the jugal forms the anterior and dorsal walls of the notch. The posterior edge of the notch is formed by the quadratojugal.

The postorbital bar, which is broad, is made up of the *postfrontal* dorsally and the *postorbital* ventrally. The dividing suture between the postorbital and postfrontal is orientated horizontally about halfway up the orbit. The postorbital forms the anterodorsal and anteroventral borders of the temporal fenestra and the posteroventral border of the orbit.

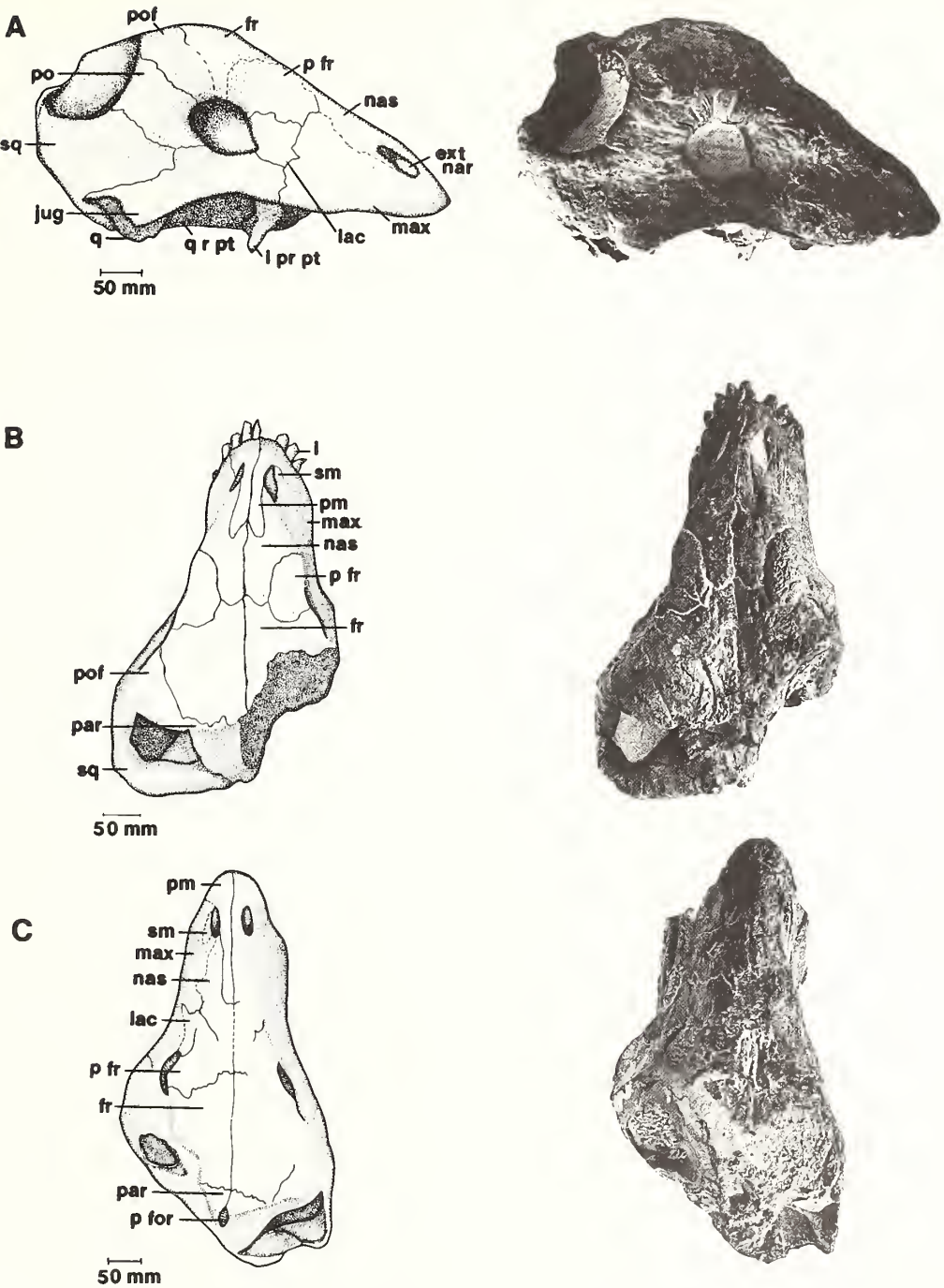
It appears that the postfrontal forms most of the dorsal margin of the temporal fenestra, with the parietal forming the posterodorsal margin. However, the suture between the postfrontal and parietal could not be identified. The *frontal* forms most of the skull roof between the orbits and temporal fenestrae. It has a laterally tapering process which forms a small portion of the dorsal border of the orbits between the prefrontal and postfrontal bones.

The *squamosal* forms the entire ventral and posterior borders of the temporal fenestra. On the ventrolateral side of the external auditory meatus the squamosal is in contact with the *quadratojugal*, while on the ventral side it meets the ascending ramus of the quadrate. Posteromedially the squamosal is in contact with the bones of the occipital region. The quadratojugal, in posterior view, is seen to form the ventrolateral corner of the skull. Dorsally its posterior surface is overlapped by the squamosal.

Dorsally, the squamosal is in contact with the *parietal*, which is badly weathered in all the specimens except NMQR 3094. A large rounded pineal foramen is situated between the temporal fenestrae. The intertemporal region becomes very narrow behind this foramen.

Occiput

As in most tapinocephaline dinocephalians, the occipital region of the skull slopes posterodorsally. The occiput is roughly flat and rectangular in shape, with the ventro-lateral regions of the *opisthotics* curving ventrally to meet the ventro-medial process of the squamosal and the dorsomedial portion of the quadrate medial to the external auditory meatus. Although the lateral and dorsal contacts of the occipital and otic bones with the tabular and postparietal bones are prominent, the sutures between the various occipital and otic bones are not easily distinguishable. The *postparietal* is an unpaired element situated dorsomedially in the occipital plate and forms a horizontal sutural contact with the parietal posterodorsally. The *tabular* is a roughly triangular bone between the postparietal, squamosal, and occipital bones with its apex extending ventrally to the point of contact between the opisthotic and squamosal. Medially it is in contact with the occipital bones.



TEXT-FIG. 2. *Tapinocanimus pamelae*. A, lateral view of NMQR 2985; B, dorsal view of NMQR 2987; C, dorsal view of NMQR 2985.

Palate

In the palate, the *premaxilla* overlies the anteroventral surface of the maxilla on the ventral side. Its posterior border extends posteromedially from a point just in front of the canine to form the anterolateral border of the internal naris. The *maxilla* forms only a small portion of the lateral border of the internal nares on the medial side of the canine and prevents contact between the palatine and premaxilla. From here it forms a thin alveolar margin which extends posteriorly to the level of the lateral flange of the pterygoid. Medially, the maxilla forms an extensive contact on the palatine and also meets the ectopterygoid.

The *vomers* are narrow vertically expanded bones which form a median trough between them. They make up the medial and posteromedial walls of the internal nares and are in contact with the premaxillae anteriorly and the palatines posterolaterally. Posteriorly they have a short pointed contact with the pterygoids.

An anteriorly directed process of the *palatine* extends almost as far as the canine tooth and forms the posterolateral, and part of the lateral, border of the internal naris. Posteromedially, the palatine forms a ventrally projecting boss which is transversely sutured to the medial pterygoid boss. The roots of several palatine teeth are situated on the anterior regions of the palatine portion of this boss in specimen NMQR 2985, and alveoli are present in specimens NMQR 2986 and NMQR 2987.

The *pterygoid* accounts for more than half the length of the palate, and the lateral flanges stretch ventrally and transversely across the palate. Posterior to the lateral flanges, the pterygoid meets its mate in the midline to form a sharp median keel. Lateral to the median keel the pterygoid is deeply excavated ventrally. On the lateral side of this wide and posteriorly flared groove, the vertically orientated quadrate ramus of the pterygoid extends posterolaterally to meet the medial condyle of the quadrate. The quadrate ramus does not extend as far as the posterior edge of the quadrate. A narrow interpterygoid vacuity is present and extends posteriorly from the level of the lateral flanges of the pterygoid. The pterygoid meets the basisphenoid immediately behind the interpterygoid vacuity.

Braincase

The *stapes* extends medially from the posterior surface of the quadrate, immediately behind the quadrate ramus of the pterygoid, to the fenestra ovalis. In ventral view, its distal end is expanded anteroposteriorly where it meets the quadrate. It becomes thinner towards the medial end which extends to the fenestra ovalis. In posterior view, the stapes is also narrower medially than laterally, and is pierced anteroposteriorly by a stapedia foramen.

The *basisphenoid* is a relatively small triangular-shaped bone with its apex pointing anteriorly to meet the pterygoid immediately posterior to the interpterygoid vacuity. A keel extends ventrally down the midline of this bone. On either side of the keel are two foramina for the carotid arteries. Posteriorly, the basisphenoid is in contact with the *basioccipital* in the anterior region of the fenestra ovalis to form the anterior edge of the fenestra.

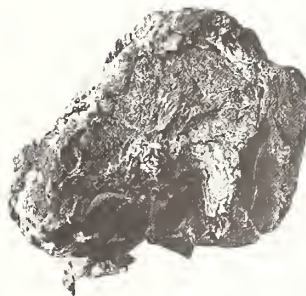
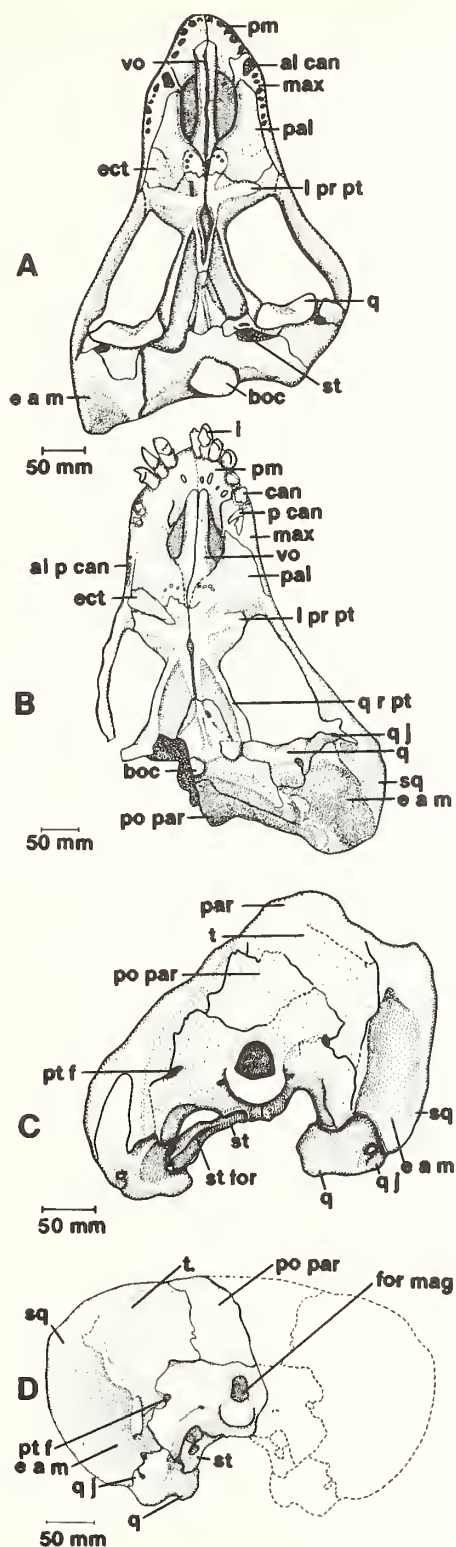
Lower jaw

The lower jaw consists of the dentary, splenial, angular, surangular, prearticular, and articular bones, but no coronoid could be recognized.

The *dentaries* are united by a symphyseal suture in the anterior midline which is very clearly defined in specimen NMQR 2987. The dentary forms the greater portion of the lower jaw. Posteriorly, it meets the *surangular* at the top of the coronoid eminence. The surangular has its greatest surface exposure on the dorso-medial side of the lower jaw, but also forms a laterally projecting ridge on the dorsolateral surface of the lower jaw. This ridge continues posteriorly as far as the ventral tip of the retroarticular process of the articular bone.

The *articular* is situated on the posteromedial side of the surangular and angular bones, and is in sutural contact with the posterior edge of the *prearticular*. The articular surface of the articular is orientated posterodorsally and has two prominent depressions which relate to the quadrate condyles. The more laterally situated depression is slightly larger than the medial one.

The *angular* meets the surangular on the dorsolateral side of the lower jaw immediately ventral to its laterally extending ridge. A prominent reflected lamina is formed by the angular and extends ventrally as far as the ventral margin of the jaw. Anteriorly, the angular is in contact with the dentary by means of a suture which slopes anteroventrally such that the angular forms a pointed contact on the ventral margin of the lower jaw between the dentary on the lateral side and the splenial on the medial side. The angular is also exposed on the ventromedial side of the posterior end of the lower jaw.



TEXT-FIG. 3. *Tapinocaninus pamelaе*. A, ventral view of NMQR 2985; B, ventral view of NMQR 2987; C, occipital view of NMQR 2985; D, occipital view of NMQR 2987.

The *splénial* is widely exposed on the medial side of the lower jaw. It attains its greatest width near its posterior end where it is in contact with the prearticular posterodorsally, and the angular posteroventrally. The splénial tapers anteriorly as the dentary becomes broader.

Dentition

Teeth are generally poorly known in South African dinocephalians (Boonstra 1962), and the dentition is not perfectly present in any of the specimens studied. In one of the skulls (NMQR 2985), all the teeth had fallen out of the alveoli prior to fossilization.

A maximum of five *incisor* teeth, all of which have talons and heels, are present in the premaxilla. A single *canine*, with no heel, is present as the first tooth in the maxilla (Text-fig. 3A, B). The crown of the canines curves backwards and the posterior edge is rounded with no sharp edge or serrations.

The canine of specimen ROZ K95 is mediolaterally compressed when compared with that of specimens NMQR 2986 and NMQR 2987 which are more rounded in section. Boonstra (1953a) records in a specimen of *Anteosaurus* that a canine close to replacement is also flattened. This may well be the situation in the present instance as the preserved canine of specimen ROZ K95 is longer than those of the other individuals. This canine is thus possibly more mature than the others, and at the point of being replaced.

The canine is followed, on the posterior side, by at least eight *postcanines* (twelve in specimen NMQR 2986, and eight in specimen NMQR 2985). The postcanine teeth have arrow-shaped crowns with small heels on the lingual side.

In the lower jaw, four incisors with crushing heels are present anteriorly in each dentary and intermesh with the incisors of the upper jaw when occluded. A single canine is present which passes on the anterior side of the canine of the upper jaw when the jaws are occluded, in the same fashion as in the Titanosuchinae. At least 15 smaller postcanine teeth are also present on the dentary, and lie lingually of the upper set when the jaws are closed.

In summary, this new dinocephalian has a heterodont dentition, consisting of incisors, canine, and postcanines, as in the Anteosaurinae and Titanosuchinae, and not homodont, as in the Tapinocephalinae (Boonstra 1953a). The dental formulae of the various specimens studied are: NMQR 2985 $I_1^5 C_1^1 PC_{14}^4$; NMQR 2986 $I_4^5 C_1^1 PC_7^{12}$; NMQR 2987 $I_4^5 C_1^1 PC_{9-10}^5$; ROZ K95 $I_7^9 C_7^1 PC_7^5$.

COMPARISON WITH OTHER DINOCEPHALIANS

Skull roof

In general shape, the skull of *Tapinocaninus* resembles that of a tapinocephaline dinocephalian as described by Boonstra (1969) and King (1988). The skull roof is greatly pachyostosed, and the postorbital bar is extremely thick, as in all the Tapinocephalinae. Because the postorbital and posttemporal bars of the Anteosaurinae and Titanosuchinae are relatively slender, the temporal fossa of these subfamilies has a relatively greater anteroposterior diameter than in the Tapinocephalinae. In the last, the thickening of these two bars produces a narrowed dorsoventrally elongated slit-like posttemporal fossa. As in anteosaurines and tapinocephalines, the temporal openings of *Tapinocaninus* are relatively large with a resultant narrow intertemporal region when compared with other forms of the Tapinocephalinae, although there are genera such as *Avenantia* and *Ulemosaurus* which do have a narrow intertemporal region. In the Tapinocephalinae, a narrow intertemporal region is considered to be primitive (Hopson and Barghusen 1986).

In dorsal view, the snout is much thinner than that of other tapinocephaline dinocephalians, except *Ulemosaurus*, but is not as long as that of the Titanosuchinae.

The quadratojugal of *Tapinocaninus* is a relatively small bone which forms part of the ventrolateral surface of the skull. In the early therapsids this bone has variable relations. However, in all of them it is much reduced in size and never enters the lower temporal arch as it does in some of the Pelycosauria. Primitively, the quadratojugal was a surface bone of the posterolateral corner of the skull flanking the quadrate. It is reduced in size and displaced medially in some of the higher sphenacodonts to rest on the quadrate dorsal to the lateral condyle (Boonstra 1971). This medial displacement is continued in the Gorgonopsia, Therocephalia, Brithopodinae, and Anteosaurinae.

In the Titanosuchinae and Tapinocephalinae the quadratojugal, variable in size and shape, still forms part of the lateral skull surface (Boonstra 1971).

The articulatory surface of the quadrate is situated ventrally below the posterior border of the orbit, a relatively anterior position which corresponds more closely with the Tapinocephalinae than the Titanosuchinae, where it is situated further posteriorly.

Occiput

In the occiput, the tabular is a triangular-shaped bone which comes to a point between the squamosal and opisthotic on the ventral side, well below the post-temporal foramen. This configuration is not present in any of the Titanosuchinae or Anteosauridae, while a similar configuration is present in some of the tapinocephalines.

Braincase

A prominent stapedial foramen is present. Among the Dinocephalia, where the stapes is known, this structure is not present in the Anteosaurinae and Brithopodinae (Boonstra 1971), but is present in some other species of the Tapinocephalinae (Boonstra 1956, 1957, 1965).

Palate

In the palate, the premaxilla forms a large proportion of the anterolateral margin of the internal nares as in the Titanosuchinae and the Estemmenosuchoidea. In the Tapinocephalinae and in *Anteosaurus*, the premaxilla has only a small contact on the anteromedial side of the internal nares. The vomers are thin bones, as in the Brithopodinae (Orlov 1958), and not broad and flat as in all other South African dinocephalians, especially the Tapinocephalinae.

A single row of palatal teeth is present on the anterior margin of the palatine bosses. Small clusters of palatal teeth are known in the Brithopodinae, Anteosaurinae, and in *Styracocephalus*, which is now considered *incertae sedis* (King 1988). Palatal teeth are normally thought not to occur in tapinocephalines: Boonstra (1936 p. 97) states 'in the gorgonopsians the palatines and pterygoids carry dentigerous ridges, whereas *no* such teeth are known in my tapinocephalid'. Boonstra (1953b) does however mention indications of roots of small palatal teeth on a rounded mound on the palatine of *Struthiocephalus*. As far as the titanosuchines are concerned, Boonstra (1963b) could not find any palatal teeth in the type of *Jonkeria ingens*.

Dentition

One of the diagnostic features of dinocephalians is the dentition, but in *Tapinocanius* the premaxillary-maxillary dentition is not perfectly preserved in any of the specimens. Boonstra (1962) states that the entire tooth (crown plus root) falls out of the alveolus before petrification most frequently in the Tapinocephalinae. In the Titanosuchinae the roots are generally preserved in the alveoli even though the crowns are frequently broken off at the level of the alveolar border either before petrification or during weathering. He considered this to be because of the difference in implantation and the mode of replacement of teeth in these two subfamilies.

The newly-discovered dinocephalian skulls have incisors with talons and crushing heels, a single canine with no heels, and numerous postcanine teeth; features of the Titanosuchinae (Boonstra 1963a). As in titanosuchine dinocephalians, the first pair of upper incisors of *Tapinocanius* is more lightly built than the others and they are laterally compressed, they lie close together and, in occlusion, they passed their talons together between the pair of lower incisors (Boonstra 1953a).

In the Titanosuchinae, the fifth upper incisor has the rear face of the talon modified to receive the lower canine with which it intermeshes. In the lower jaw, the fourth incisor is somewhat weaker than the anterior ones (Boonstra 1962). In the Anteosaurinae, the fifth upper incisor passes labially to the lower canine during occlusion and not anteriorly, and the two teeth consequently do not intermesh (Boonstra 1962). In the new dinocephalian, the lower canine in specimen NMQR 2986 (the only one where it is preserved) is situated more in the titanosuchine position, passing in front of the upper canine (Text-fig. 1b). The size of the upper canine of *Tapinocanius* (diameter at

alveolar border, 19–21 mm anteroposteriorly, and 13–18 mm mediolaterally; crown length, 46–52 mm) is much smaller than that of equivalent-sized titanosuchine dinocephalians (diameter at alveolar border, 35–50 mm anteroposteriorly, and 21–36 mm mediolaterally; crown length, 60–110 mm) (Boonstra 1962).

As is the case in titanosuchine dinocephalians (Boonstra 1962), the postcanines of the lower jaw of *Tapinocanius* are situated on the lingual side of those of the upper jaw when the jaws are closed, and do not intermesh as in tapinocephaline dinocephalians. The number of postcanine teeth in the Anteosaurinae and Titanosuchinae varies greatly, from one to nineteen, and is of doubtful systematic value as it can even vary from the left to right side of the jaw (Boonstra 1953a).

The postcanines of the lower jaw of *Tapinocanius* more closely resemble those of the Tapinocephalinae than the Titanosuchinae in that the labial portion of the crown is slightly bulbous, and there are small heels on the lingual side.

Despite having heterodont titanosuchine-like dentition, the skulls display many tapinocephaline features such as postcanines with talon and heel (Boonstra 1963a), the pachyostosed skull roof and form of the postorbital bar, relatively anterior position of the quadrate (Boonstra 1963b), and orientation of the tabular bone. It is thus reasonable to consider this dinocephalian as belonging to the Tapinocephalinae but still retaining some plesiomorphic characters which are not present in any other known tapinocephaline dinocephalian.

TAXONOMIC IMPLICATIONS

Several palaeontologists have addressed the problem of classification of the Dinocephalia, but only recently has a cladistic approach been used. Kemp (1982) was the first to use such an approach but did not give characters relating to the sister groups contained in his cladogram. Hopson and Barghusen (1986) undertook a cladistic analysis of therapsid relationships and included the various dinocephalian infraorders, while King (1988) also drew up a cladistic analysis of the Dinocephalia. All consider, as was previously stated by Boonstra (1965), that the Anteosaurinae are the most primitive of the South African dinocephalians, and the Tapinocephalinae are the most derived. The Titanosuchinae fall between the two. The scheme proposed by Hopson and Barghusen (1986) differs from that of Kemp (1982) and King (1988) in the position of the Estemmenosuchoidea. This however does not have any bearing on this paper and will not be discussed further.

Hopson and Barghusen (1986) use the following apomorphies of the Tapinocephalinae to separate them from the Titanosuchinae:

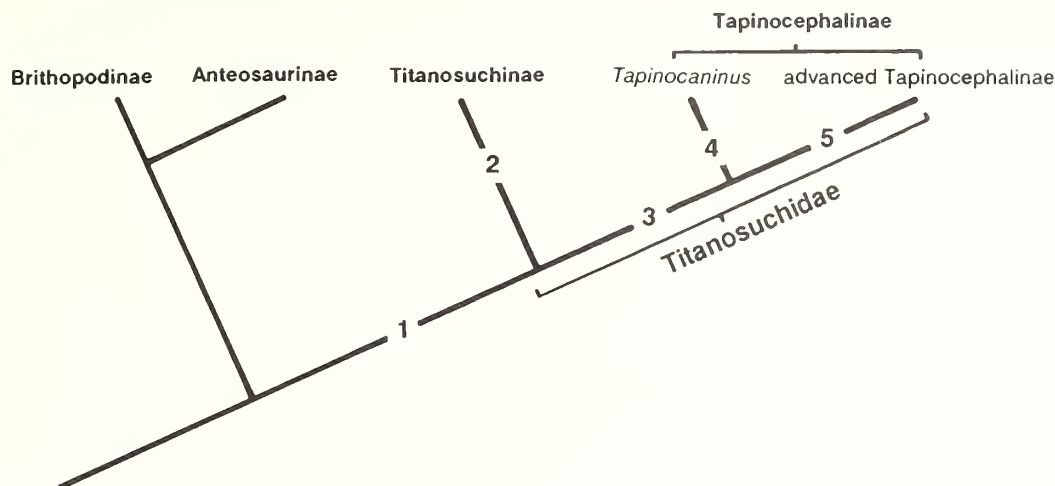
1. canines incisiform;
2. pattern of interlocking extends to canines and postcanines;
3. anterior end of postcanine row does not extend lingual to the canine.

A reassessment of material of the Tapinocephalinae and Titanosuchinae housed in South African Institutes has revealed that character 3 is shared by both of these groups and is not an apomorphy of the Tapinocephalinae alone.

King (1988) uses the following apomorphies of the Tapinocephalinae to separate them from the Titanosuchinae. Character 2 corresponds with that of Hopson and Barghusen (1986):

1. heels on the incisor teeth expanded;
2. all teeth interdigitating;
3. size of temporal fossa reduced due to pachyostosis.

Of all these characters, *Tapinocanius* possesses only the first character of King (1988), and hence it is considered the most primitive representative of the Tapinocephalinae known. As a result, it is necessary to broaden the concept of what is presently considered to be a tapinocephaline dinocephalian (Text-fig. 4).



TEXT-FIG. 4. Cladogram illustrating the relationships of *Tapinocaninus* to the Titanosuchinae and Tapinocephalinae (modified after King 1988). Apomorphies for each node are: 1 (defining Titanosuchidae), enlarged heel on incisor teeth; jaw hinge slightly anteriorly placed to be positioned below postorbital bar; lower canine reduced in height; lower canine positioned anterior to upper one when jaws closed. 2 (defining Titanosuchinae) (after King 1988), many leaf-shaped and serrated postcanine teeth. 3 (defining Tapinocephalinae), heel on postcanine teeth; pachyostotic thickening of postorbital bar and skull roof. 4 (autapomorphies of *Tapinocaninus*), vomer narrow in ventral view; premaxilla extends far posteriorly to almost touch palatine resulting in maxilla having very short contact on lateral border of internal nares. 5 (defining advanced Tapinocephalinae), reduced canine tooth; quadrate further anteriorly positioned to be situated below orbit; all teeth interdigitating; size of temporal fenestra reduced due to pachyostosis.

CONCLUSION

A new genus and species of tapinocephaline dinocephalian, *Tapinocaninus pamela*, has been discovered from the lowermost rocks of the Beaufort Group in the same zone as the primitive dicynodont *Eodicynodon* (Rubidge 1987), and *Patranomodon*, the most primitive anomodont known (Rubidge and Hopson 1991). *Tapinocaninus pamela* is the most primitive member of the Tapinocephalinae yet discovered and retains several plesiomorphic titanosuchine-like characters which are not present in any other known tapinocephaline dinocephalians. This has led to modifications of cladistic characters previously used (Hopson and Barghusen 1986; King 1988) to separate the Tapinocephalinae from the Titanosuchinae.

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ABBREVIATIONS USED IN THE TEXT FIGURES

al.can.	alveolus for canine	p.can.	postcanine
al.p.can.	alveolus for postcanine tooth	p.fr.	prefrontal
art.	articular	p.for	pineal foramen
boc.	basioccipital	pm.	premaxilla
can.	canine	po.	postorbital
den.	dentary	pof.	postfrontal
e.a.m.	external auditory meatus	po.par.	postparietal
ect.	ectopterygoid	pt.f.	posttemporal foramen
ext.nar.	external nares	q.	quadrate
for.mag.	foramen magnum	q.j.	quadratojugal
fr.	frontal	q.r.pt.	quadrate ramus of pterygoid
i.	incisor	ref.l.	reflected lamina
jug.	jugal	sm.	septomaxilla
lac.	lachrymal	sq.	squamosal
l.pr.pt	lateral process of pterygoid	st.	stapes
max.	maxilla	st.for.	stapedial foramen
nas.	nasal	t.	tabular
pal.	palatine	vo.	vomer
par.	parietal		

FISHES AND AMPHIBIANS FROM THE LATE PERMIAN PEDRA DE FOGO FORMATION OF NORTHERN BRAZIL

by C. BARRY COX and P. HUTCHINSON

ABSTRACT. The vertebrate fauna of the Pedra de Fogo Formation of northern Brazil includes a palaeonisciform fish *Brazilichthys macrognathus* gen. et sp. nov., which is placed in a new family, the Brazilichthyidae. Other fishes include fragments of ctenacanth and xenacanth sharks, edestid holocephalians, and dipnoans. Tetrapods include the archegosaurid amphibian *Prionosuchus plummeri*, which is compared with other archegosaurs. Its extremely long narrow snout suggests that the Pedra de Fogo Formation is of Late Permian age, rather than Early Permian. A large specimen of *Prionosuchus* is probably the longest amphibian currently known.

THE Pedra de Fogo Formation lies in the Maranhão-Piauí (or Parnaíba) Basin of northern Brazil, which covers parts of the state of Maranhão and adjoining states and which originated in the Siluro-Devonian. Permo-Carboniferous sediments deposited in this basin have, over the past thirty years, been given various names. The most common nomenclature today recognizes a Late Carboniferous Piauí Formation, which is overlain by the Pedra de Fogo Formation. The latter is overlain by the Motuca Formation, which is currently regarded as of Triassic age.

The Pedra de Fogo Formation was named after the small stream that runs through the area; the name is derived from the large amount of flint (firestone, or 'pedra de fogo' in Portuguese) which is found in its bed. The Formation was first recognized and defined by Plummer (1948), following the geological traverse of the Basin made by Plummer, Price and Gomes in 1946. In brief visits during 1945 and 1946, Price found fish and amphibian remains south of the township of Pastos Bons. The amphibian, which Price (1948) named *Prionosuchus plummeri*, was the first temnospondyl described from South America.

As Price concluded, the very elongate snout of *Prionosuchus* suggested that it belonged to the early group of long-snouted temnospondyls called archegosaurs, known from Permian sediments in Europe. The fish remains from the Pedra de Fogo Formation included the fin-spines of ctenacanth sharks, the teeth of xenacanth sharks, palaeoniscoid scales, coprolites and, at a lower level in the Formation, remains of the marattalian tree-fern *Psaronius*. Price (1948) concluded that the Pedra de Fogo Formation was certainly of Permo-Carboniferous age, and that it was most probably of Early Permian age.

The suggestion that *Prionosuchus* was of Early Permian age was of some interest, for it was the only Early Permian amphibian known from South America, and indeed one of the very few tetrapods known from the Early Permian of Gondwanaland (Cox 1974).

The Pedra de Fogo Formation therefore seemed to merit further investigation, and two visits to the Maranhão Basin were made. A reconnaissance in 1970 by L. I. Price of the Departamento Nacional de Produção Mineral, Rio de Janeiro, and J. Attridge of Birkbeck College, London, found a few fragments of amphibian. A larger party, consisting of the senior author and Attridge, together with Price and his assistant D. A. Campos, visited the area in 1972. The fish and amphibian remains described in this paper were found in the area where Price found *Prionosuchus*, east of the road between Pastos Bons and Nova Iorque (lat. 6° 35' S, 44° 2' W), and mainly up to 300 m east of those parts of the road that lie between 5.6 and 6.7 km south of the junction of that road and the main Highway BR-230 at Pastos Bons. A few fragments were also found east of a point 8.7 km

south of that junction. Geological maps today show the Pedra de Fogo Formation both to the east and to the west of Pastos Bons. However, both these areas were unproductive, despite aerial search for exposures, followed by ground search.

GEOLOGICAL BACKGROUND

Plummer (1948) stated that the Pedra de Fogo Formation, 10–20 m thick, was made up of alternating deposits of silt, limestone, and chert, the last predominating and forming beds and spherical concretions. The limestones contain oolites and pisolites, the silt layers contain the vertebrate fossils, and the chert beds contain edgewise, intraformational, fragmental conglomerates and, in some layers, large pieces of petrified wood. The chert also has an oolitic and pisolitic texture, and both Lisbôa (1914) and Plummer (1948) stated that the rocks were originally limestone and had later been changed to chert by chemical replacement, perhaps following deposition of a layer of volcanic ash over the region during the Early Cretaceous, when diabase was intruded into the earlier deposits.

Plummer (1946, fig. 2) drew a section in the Pedra de Fogo Formation 6.6 km south of the township of Pastos Bons, near the road to Nova Iorque. He showed it there to lie upon the upper part of the Floriano Formation (now included as part of the Piauí Formation), which consisted of grey marine shales interbedded with thin-bedded sandstones containing chert. Plummer stated that the Floriano Formation was of Late Pennsylvanian or Early Permian age. His figure showed that, in this region, the Pedra de Fogo Formation was unconformably

TABLE 1. Section through the upper part of the Pedra de Fogo Formation.

Height above base of Formation, in metres	Thickness in metres	
14.05	0.40	Basal conglomerate of Pastos Bons Fm.
13.65	1.45	Purple shale with subspherical concretions
12.20	0.30	Thin (0.002–0.005 m) layer of calcite
11.90	2.15	Purple siltstone, as below Thin (0.01 m) layer of calcite Purple siltstone, as below, including a 0.05 m layer of haematite with bone fragments
9.75	4.05	Thin (0.01 m) layer of calcite Finely bedded purple siltstone, with intercalations of greenish shale and of coarse sandstone with silica matrix. Occasional fragments of fossil wood.
5.70	1.60	Finely stratified greenish sandstone, as below.
4.10	0.30	Moderately stratified, light-coloured, poorly sorted sandstone.
3.80	2.90	Very fine greenish siliceous sandstone with cross-lamination
0.90	0.90	Fine siliceous purple sandstone.
0		Bed of large flints at bridge.

overlain by the Melancieiras Formation (now known as the Pastos Bons Formation, and considered as Middle-Late Jurassic in age; Pinto and Purper 1976). However, Plummer (1946, fig. 3) also described a section of the Pedra de Fogo Formation further east, between São Domingos and Benedito Leite, where he found that the Pedra de Fogo Formation was unconformably overlain by the dark brick-red sandstones of the Motuca Formation. He stated (1948, pp. 107–108) that the Motuca Formation was separated from the Pedra de Fogo Formation by an erosional unconformity, and that it was overlain by the Melancieiras Formation (now known as the Sambaiba Formation; Brito 1981). Plummer regarded the age of the Motuca Formation as uncertain, and it has been ascribed variously to the Late Permian or to the Triassic (Brito 1981; Medeiros, pers. comm., 1988).

A section was taken of the upper part of the Pedra de Fogo Formation, in the bed of the Pedra de Fogo stream where it ran under the Pastos Bons–Nova Iorque road at a point 6.6 km south of the junction of that road with Highway BR-230 (Table 1).

The vertebrate fauna of the Pedra de Fogo Formation comprises fin-spines of ctenacanth sharks and teeth of xenacanth (pleuracanth) sharks (Santos 1946), teeth of edestid holocephalians, dipnoan teeth, scales and cranial remains of palaeoniscoid fish, and the remains of temnospondyl amphibians (one of very large size). This fauna was found below a layer of fossiliferous haematite that occurred about 11.9 m above the base of the section. Most of the bones were free of haematite.

The levels of haematite and calcite, and the apparently lacustrine nature of the sediments, suggest a fresh-water environment of deposition. The ctenacanth and xenacanth sharks, which are elsewhere characteristic of fresh-water environments, is confirmatory evidence of this. The bone fragments are mostly badly worn, and the sediments had clearly been water-sorted and transported, fragments of similar size and density being found together. The overall impression is therefore one of deposition in the lower reaches of a river system. The large size of some of the vertebrates indicates that the body of water inhabited by these elements of the fauna must have been extensive, suggesting a deltaic environment including deep rivers or lakes.

The fin-spines and fish teeth from the Pedra de Fogo Formation are currently being studied by Dr Silva Santos of the DNPM. The description of the palaeoniscoid skull (below) is the work of the late Dr P. Hutchinson; the remainder of this paper is the work of the senior author (C.B.C.). Institutional abbreviations are: BMNH, British Museum (Natural History), London; DNPM, Departamento Nacional de Produção Mineral, Rio de Janeiro.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII

Order PALAEONISCIFORMES

Family BRAZILICHTHYIDAE fam. nov.

Diagnosis. As for genus.

Genus BRAZILICHTHYS gen. nov.

Type species. *Brazilichthys macrognathus* nov.

Brazilichthys macrognathus sp. nov.

Text-fig. 1

Horizon and locality. Pedra de Fogo Formation, state of Maranhão, N. Brazil. Found about 100 m east of the Pastos Bons–Nova Iorque road, about 6 km south of Pastos Bons.

Holotype. DNPM 1061-P, the only known specimen.

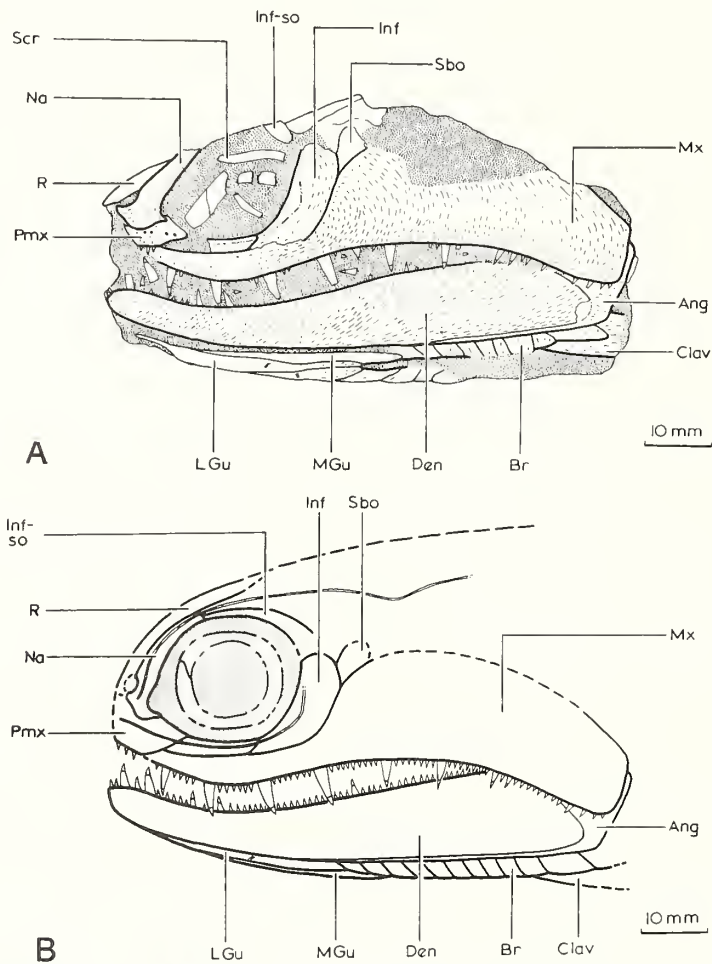
Diagnosis. Upper jaw margin strongly convex below orbit; teeth arranged in two series, the inner row composed of long, slightly recurved, conical teeth; median and lateral gulars almost half as long as the lower jaw. The genus is incompletely known, and this diagnosis must be regarded as provisional.

Description. The skull of *B. macrognathus* is represented by a single specimen, 80 mm long and 42 mm deep.

The dermal bones of the skull roof and opercular region are missing, but the other bones are well preserved, especially on the left side (Text-fig. 1A). The restoration (Text-fig. 1B) is based mainly on the left side of the specimen, but some additional details are derived from its right side.

The postorbital part of the maxilla is long and indicates that *B. macrognathus* had an inclined suspensorium. The part of the maxilla exposed below the orbit is extremely narrow, its dorsal edge being overlapped by the infra-orbital series and its ventral edge being separated from the upper jaw margin by a long premaxilla. The teeth of the upper jaw are arranged in two series: an inner series of eight or nine striated, conical teeth that are up to 6 mm long, and an outer series of more numerous teeth that are about 0.5 mm long. The larger teeth are terminated by small enamel caps similar to those described in *Pteronisculus* (*Glaucolepis*) by Nielsen (1942), and in *Nematoptychius* by Gardiner (1963).

The posterior and ventral edges of the orbit are bordered by two infra-orbitals. The anterior infra-orbital is slightly expanded at its anterior end (part of this bone was removed during preparation in order to expose details of the snout), while the posterior infra-orbital is broad and lunate. The dorsal edge of the orbit is bordered by a slender, curved element that extends anteriorly to meet the nasal. It is identified here as an infraorbito-supraorbital (dermosphenotic of other authors, e.g. Moy-Thomas and Dyne 1938; Gardiner 1963).



TEXT-FIG. 1. *Brazilichthys macrognathus*, gen. et sp. nov. Lateral view of skull, natural size. A, holotype, DNPM 1061-P. B, restoration of skull. Abbreviations: Ang, angular; Br, branchiostegal ray; Clav, clavicle; Den, dentary; Inf, infra-orbital (dermosphenotic); Inf-so, infraorbito-supraorbital; L Gu, lateral gular; M Gu, median gular; Mx, maxilla; Na, nasal; Pmx, premaxilla; R, rostral; Scr, sclerotic ring; Sbo, suborbital.

Objections to this view have already been put forward (Hutchinson 1975). It is also uncertain whether the infraorbital-supraorbital meets the posterior infraorbital, because the posterior edge of the latter bone is imperfectly preserved; however, comparison with other palaeoniscoids suggests that these bones did, in fact, meet to complete the posterior edge of the orbit.

The snout is composed of a rostral and paired nasals, premaxillae, and antorbitals. The rostral is identified as such in view of Patterson's (1975) conclusion that the median snout element in chondrosteans, identified as the post-rostral by many authors (e.g. Gardiner 1963, 1967 in palaeoniscoids; Hutchinson 1973 in redfieldiids and perleidids), is homologous with the rostral of holosteans and pholidophorids. Close to its ventral end, the nasal bears notches for the anterior and posterior nasal apertures. The premaxillae are unique among chondrosteans because they extend posteriorly almost to the level of the posterior orbital edges, and because they are separated at the tip of the snout. The antorbital is large and bears the ethmoid commissure of the infraorbital sensory canal. The antorbital branch is either absent or so poorly preserved that its course is not visible. The posterodorsal edge of the antorbital borders the orbital edge, and its posteroventral edge either butts against, or overlaps, the anterior ends of the anterior infra-orbital, the maxilla and the premaxilla. Its ventral edge bears the two types of teeth identified on the maxilla and premaxilla. The extreme anterior end of the antorbital is missing, so that the structure of the tip of the snout is unknown, but it appears likely that the antorbitals met at the midline of the snout.

There is an incompletely preserved suborbital wedged between the posterior infra-orbital and the dorsal part of the maxilla.

The lower jaw is long, and curves dorsally towards the symphysis. This curve is reflected in the shape of the edge of the upper jaw and does not appear to be due to post-mortem distortion. The teeth of the lower jaw are similar to those of the upper jaw, but are somewhat shorter. The angular extends along half the length of the lower jaw, but is almost completely overlapped on the lateral surface by the dentary, which is extremely thin posteriorly. There are three gular plates, which together are almost half the length of the lower jaw. The lateral gular plates bear short pit lines, but similar pit lines are not visible on the median gular. At least nine branchiostegal rays are present between the gular plates and the level of the posterior end of the lower jaw.

The known dermal bones of the skull bear an ornament of ridges and tubercles, and their distribution is indicated in Text-fig. 1.

[The form of the teeth and the elongated maxilla suggest that the family Brazilichthyidae may be related to the Permian family Acrolepididae (Gardiner and Schaeffer 1989); note suggested to senior author by Dr B. Gardiner, 1989.]

Class AMPHIBIA
Order TEMNOSPONDYLI
Family ARCHEGOSAURIDAE
Genus PRIONOSUCHUS Price, 1948
Prionosuchus plummeri Price, 1948

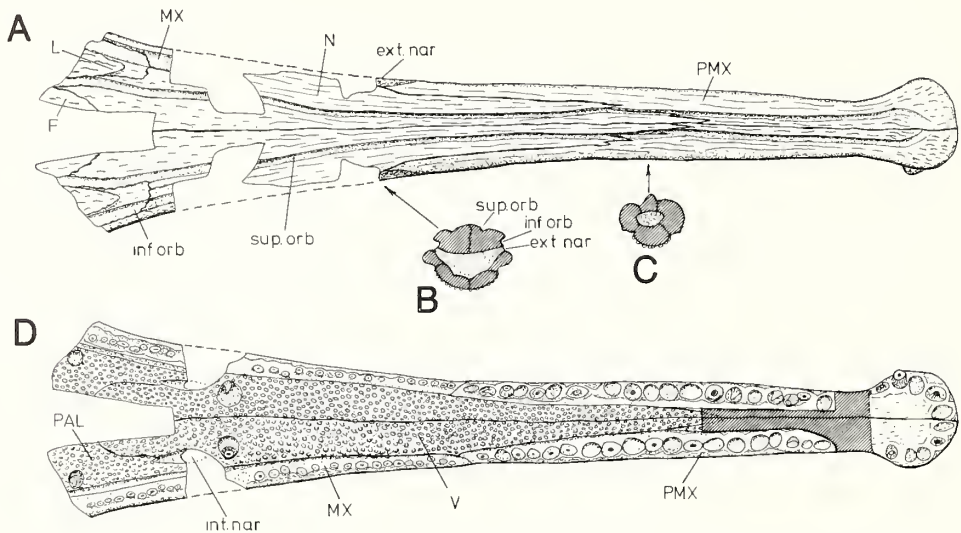
Text-fig. 2

Material. The genus was established by Price on the basis of a rostrum, a fragment of mandible and a femur (DNPM 320-R), all from the Pedra de Fogo Formation south of Pastos Bons. Price noted that the elongate rostrum resembles that of the archegosaur *Platyoposaurus*, but that it is proportionately much longer and more laterally compressed than that of *Platyoposaurus*. (The latter genus was originally named *Platyops* by Twelvetrees (1880) but, as noted by Lydekker (1889, p. xi), that name was preoccupied for a fish. Lydekker accordingly renamed the archegosaur *Platyoposaurus*.) Price also noted that the nasals, maxillae and palatines of the Brazilian specimen extend further forward than those of *Platyoposaurus*, and that the external nares are smaller and more laterally placed. He therefore established the new genus *Prionosuchus*. The rostrum of the holotype specimen is 345 mm long, and Price estimated that the complete skull would have been about 500 mm long.

Price collected scraps of two further rostra in the same area in a short visit in 1948 (DNPM 862-R, 863-R), and the 1970 reconnaissance collected further scraps, including a right mandibular ramus (DNPM 864-R) and two intercentra (DNPM 865-R). The following amphibian remains were collected during the 1972 expedition: BMNH R12000, the mid-portion of a rostrum; BMNH R12001, the posterior part of a rostrum; BMNH R12002, a median fragment of the frontal region of a slightly smaller skull; BMNH R12003, many fragments of a small skull; BMNH R12004, fragments of vertebrae, including pleurocentra and intercentra, and fragments of skull, and BMNH R12005, fragments of skull and post-cranial skeleton. The last specimen is nearly three times the size of most of the other amphibian specimens.

Description. Though the large specimen provides additional information on the anatomy of the posterior region of the skull and also contains portions of the rostrum, it is so fragmentary that the anatomy of the anterior part of the skull can be most reliably reconstructed using the fragments of the smaller skulls, and this is then used as a basis for estimating the size of the larger specimen.

Price's holotype specimen (DNPM 320-R) includes an almost complete rostrum, from the anterior tip back to a point slightly behind the internal nares. Anterior to the suture between the premaxilla and the maxilla, the rostrum is about 20 mm thick dorso-ventrally, and about 23 mm wide. Posterior to that suture, it widens to 31 mm at its posterior end but becomes only 17 mm thick dorsoventrally. The dorsal and the ventral surface are both flattened. The rostrum bears the anterior continuation of the supra-orbital sensory canal. The palatal surface of the vomers and palatines is covered with a fine shagreen of conical denticles. The expanded tip of the rostrum bears large teeth; immediately posterior to this, there is a constricted region bearing small teeth. Behind this constricted region, and as far back as the palatal portion of the premaxilla-maxilla suture, the teeth are of moderate size. Posterior to this suture, the teeth revert to smaller size. A pair of vomerine fangs and a pair of palatal fangs lie respectively anterior and posterior to the internal nares.



TEXT-FIG. 2. A, Dorsal and D, ventral views of the snout of *Prionosuchus plummeri* $\times \frac{1}{3}$, reconstructed from the type specimen (DNPM 320-R) and from the postero-lateral fragment (DNPM 862-R). B, C, Cross-sections of the snout at the positions shown, from specimen BMNH R12001. Abbreviations: F, frontal; L, lacrimal; MX, maxilla; N, nasal; PAL, palatine; PMX, premaxilla; V, vomer; ext.nar, external nares; int.nar, internal nares; inf.orb, infra-orbital sensory canal; sup.orb, supra-orbital sensory canal.

BMNH R12001 is a 105 mm long section of the middle portion of a rostrum of similar size. It differs from this region of the holotype only in that it is less flattened, being oval in cross-section, 24 mm thick and 34 mm wide, the palatal surface being convex (Text-fig. 2B, C). This suggests that the flattened form of the holotype was due to post-mortem crushing which collapsed the internal narial passage.

DNPM 862-R consists of two portions of rostrum, dorsoventrally crushed like the holotype. The anterior portion corresponds to the most posterior portion of the holotype, including the region of the internal nares and the posterior part of the external nares. The former appear to have been elongate and about 20 mm long; the dorsal and ventral regions of the specimen have therefore become broken apart from one another in this area. The palatal teeth are noticeably larger anterior to the internal nares than more posteriorly. The supra-orbital sensory canals are very well-developed, being up to 4 mm deep, and diverge posteriorly.

The more posterior part of DNPM 862-R is separated from the anterior part by a gap which ventrally appears to have been only a few millimetres wide. Ventrally, this part shows the posterior end of the internal

nares and, 18 mm behind this, the socket of the fang on the anterior end of the palatine bone. Dorsally, this part shows the nasal-frontal suture, the anterior end of the lacrimal bone, and two sensory canals. The more medial of these canals appears to be the posterior part of the supra-orbital canal. The more lateral canal is probably the infra-orbital sensory canal which, on BMNH R12001, can be seen to continue anteriorly and die out c. 30 mm anterior to the external nares.

BMNH R12000 and R12001 are uncrushed and show a series of cavities, filled with fine yellowish matrix, which extend through the snout. The posterior end of the rostrum fragment BMNH R12001 shows a section just anterior to the external nares (Text-fig. 2B); it shows a matrix-filled cavity extending from the external nares into the centre of the rostrum. The anterior end of the same specimen (Text-fig. 2C) shows a large central matrix-filled cavity, which presumably extended to the anterior end of the snout. Posterior to the external nares, the cavity formed the narial passage, which presumably ended at the internal nares. However, a fragment of the median portion of a small skull including the anterior part of the frontals (BMNH R12002) shows two smaller pairs of matrix-filled cavities extending posteriorly into the skull. In life, all these cavities were presumably filled with air and acted as flotation device for the head, rather like the cavities of the crocodilian skull.

Restoration and comparison. The fragments described can be used to produce a restoration of the anterior part of the skull of *Prionosuchus plummeri* (Text-fig. 2), which was about 380 mm long. Comparison of the sutural pattern of the snout of *Prionosuchus* with that of its closest known relative, *Platyoposaurus* (Text-fig. 3e) shows that the further elongation of the snout of the former has been achieved primarily in the region of the external nares. The nasals of *Platyoposaurus* end abruptly, at the level of the anterior end of the external nares. Those of *Prionosuchus* extend further forwards, gradually tapering to a narrow point, beyond which the snout is composed exclusively of the premaxillae. On the other hand, the lacrimals of *Platyoposaurus* nearly reach the external nares, while those of *Prionosuchus* hardly extend beyond the anterior end of the frontals, doubtless because of the great narrowing of the skull.

An estimate of the total skull length of *Prionosuchus* can be made by comparing it with that of *Platyoposaurus*. It would be possible simply to assume that the position of the naso-frontal suture was unchanged, and to enlarge a drawing of a *Platyoposaurus* skull until its width at this point was equal to that of the *Prionosuchus* skull. However, this may be an over-simple approach. The elongate snout of *Prionosuchus*, with its enlarged, spatulate tip, is identical to that found in the fish-eating gharial crocodiles of today. The narrowing of the snout reduces water-resistance when closing the jaws, and therefore allows the closure to take place more rapidly – an obvious advantage, especially when snapping at fish. Some of this advantage would be lost if the posterior end of the snout widened only gradually to match the width of the more posterior part of the skull, and this may be the reason why the snout of the gharial widens more abruptly. It seems likely that this would have been a factor also in the evolution of the snout of *Prionosuchus*, and the most posterior preserved part of its snout does indeed appear to curve outwards quite noticeably. In the reconstructed skull (Text-fig. 3F), it has therefore been assumed that the frontals do not project as far anteriorly as in *Platyoposaurus*, and the snout is shown as widening fairly abruptly. It is also possible that the coinciding anterior terminations of the lacrimal and of the frontal mark the level at which the skull narrowed abruptly into a snout dominated by the nasal, maxilla, and premaxilla. A reduction in the number of sutural joints in this latter structure would also increase its strength. It is possible that the degree of shortening of the immediately pre-orbital region that is shown in the reconstruction is incorrect, but there is at present no way in which this can be verified. As reconstructed in this manner, the total skull length of *Prionosuchus* based on these specimens would have been about 580 mm.

Post-cranial skeleton. A number of isolated amphibian pleurocentra and intercentra have been found in the Pedra de Fogo Formation, and show that *Prionosuchus* had a rhachitomous vertebral column similar to that known in other archegosauroids, such as *Archegosaurus* (Hofker 1928) and *Platyoposaurus* (Konzhukova 1955). The intercentra are up to 30 mm wide, and the pleurocentra are 20 mm high.

The large specimen of Prionosuchus. During the 1972 expedition, a much larger specimen of *Prionosuchus*

(BMNH R12005) was collected in the Pastos Bons locality. Though extremely incomplete, it included fragments of skull, vertebrae, ribs, scapulae, cleithra, clavicles, ilium, ischium, and femur.

The skull material includes fragments of the rostrum and palatal bones, both quadrates and parts of the margins of the orbits and otic notch. It is particularly interesting that one fragment shows the supratemporal bone entering the otic notch and so separating the tabular from the squamosal, as in *Archegosaurus*. The fragments show the expanded anterior end of the rostrum found in both *Prionosuchus* and *Platyoposaurus*, and the shagreen of palatal teeth characteristic of the former. The fragments also include a number of small, subcircular platelets of bone, up to 14 mm in diameter and 2 mm thick, with smooth, slightly convex under surfaces. Each platelet bears up to 30 denticles. They were probably embedded in the soft tissues of the mouth (for example, in the tissues overlying the interpterygoid vacuities), so that these areas, like the palatal bones, were denticulated and could grip the prey.

Despite the difference in size, there can be little doubt that this specimen belongs to *Prionosuchus*. The only part of it that is sufficiently complete to provide a basis for an estimate of its size when complete is the tip of the rostrum. This is 100 mm across, while that of the holotype specimen is only 35 mm across. As already mentioned, the snout of *Prionosuchus* is very like that of the modern fish-eating gharial crocodiles. Though the relative length of the snout of these crocodiles increases rapidly in early ontogeny, it remains almost constant from a skull length of 400 mm up to that of the largest specimen measured, 800 mm (data from Kálin 1933, tables II and III). It therefore seems reasonable to assume that proportions of *Prionosuchus* did not change greatly between the smaller (but definitely adult) specimens and the large specimen, in which the skull of the latter would have been about 1.6 m long.

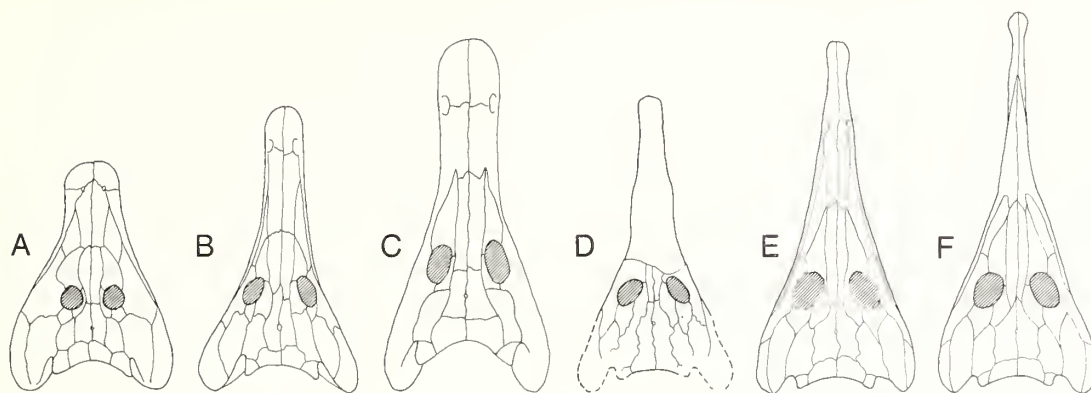
Other archegosauroids, such as *Archegosaurus* and *Platyoposaurus* (Konzhukova 1955) had an elongate body and tail but small limbs. Though the skeleton of *Platyoposaurus stuckenbergi* that Konzhukova describes is incomplete, the first 9–10 vertebrae have a length approximately equal to $\frac{2}{3}$ the skull length. They are followed by another nine vertebrae with snout centra and ribs, with no sign of diminution in size towards the sacral region. There therefore seems little doubt that the body alone of such an archegosauroid was considerably longer than the skull.

Prionosuchus certainly had small limbs, for the incomplete femora of the large specimen show that the complete bone could not have been more than 15 mm in diameter and 130 mm long. This indicates that it did not swim by means of enlarged, paddle-like limbs, but instead swam like a crocodile, by means of lateral undulations of the body and elongate tail. Wermuth (1964) has analysed the relationships between head, body and tail length in modern crocodilians. The largest gharial measured by him had a skull 0.83 m long, with a body 2 m long and a tail 2.65 m long – a total of nearly 5.5 m. Even if the snouts and body-plus-tail lengths of larger specimens of gharial or *Prionosuchus* were proportionately smaller than in specimens of intermediate size, there still seems little doubt that the large specimen of *Prionosuchus*, with a skull twice the length of that of Wermuth's largest gharial, must have had a total length greater than that of the gharial. There therefore seems little doubt that it was considerably larger than the longest amphibian presently recorded, *Eogyrinus attheyi* (Panchen 1972), which had an estimated total length of 4 m.

THE RELATIONSHIPS OF *PRIONOSUCHUS* AND THE AGE OF THE PEDRA DE FOGO FORMATION

As Price (1948) suggested, *Prionosuchus* is an archegosauroid: the great, slender elongation of the skull and the contact between the lacrimal and the frontal agree with Romer's (1947) definition of that family, in which he included three genera: *Archegosaurus*, *Melosaurus* and *Platyoposaurus*. Two other genera, *Bashkirosaurus* and *Collidosuchus*, were added by Gubin (1981, 1986).

The earliest member of the Archegosauroidae is *Archegosaurus* itself (Text-fig. 3B). The type species, *A. decheni* (Hofker 1928; Whittard 1928), is from the ironstone nodules of the Lebach Group of the Saar region of Germany, of early Lower Permian age. Other specimens of *Archegosaurus*, named *A. ornatus* (Woodward 1905) and *A. kashmiriensis* (Tewari 1962) have been found in the Lower Gondwana deposits of Kashmir, which are probably also of Early Permian age.



TEXT-FIG. 3. The skulls of archegosauroids, drawn to similar widths across posterior portion of the skull. A, *Melosaurus*, from Romer 1947. B, *Archegosaurus*, from Romer 1947. C, *Collidosuchus*, from Gubin 1986. D, *Platyoposaurus stuckenbergi*, after Efremov 1933 (his dorsal view, fig. 1, superimposed on his ventral outline, fig. 3). E, *Platyoposaurus watsoni*, after Efremov 1933. F, *Prionosuchus* (see text for details of reconstruction).

The other archegosauroid genera, *Melosaurus*, *Bashkirosaurus*, *Collidosuchus*, and *Platyoposaurus*, are found in early Late Permian (Kazanian) deposits west of the southern Urals, in European Russia. The archegosauroids are found in Zones I and II of the deposits (which are numbered from the base upwards).

Melosaurus (Meyer 1860) was originally placed in the Archegosauroidae because of its somewhat elongate preorbital region (Text-fig. 3A). However, this region is still comparatively short, being less than 50% of the total skull length, and is much wider than that of *Archegosaurus* (Text-fig. 3B). It is clearly not merely a juvenile archegosauroid, as Hartman-Weinberg (1939) suggested, since skulls up to 400 mm long are now known.

Collidosuchus (Gubin 1986) has a snout whose elongation is intermediate between that of *Archegosaurus* and that of *Platyoposaurus* (Text-figs 3B–D). This is due in part, at least, to the appearance of a growth zone just anterior to the external nares, which consequently lie further back than in *Archegosaurus*, though not as far back as in *Platyoposaurus*.

Gubin had earlier (1981) described another Late Kazanian archegosauroid, *Bashkirosaurus*, but this specimen comprises only the median part of the skull from the orbits posteriorly. Rather surprisingly, Gubin does not mention this specimen in his later (1986) paper on *Collidosuchus*.

The genus which Lydekker (1889) renamed *Platyoposaurus* (see above, p. 565) was erected by Twelvetrees (1880) on the basis of a badly-damaged skull which he named *P. rickardi*. The snout of this specimen is lacking, and it seems unlikely that it shows any characters which would allow other specimens to be placed in this species. The name *Platyoposaurus rickardi* should therefore be applied only to the type specimen.

In 1884, Trautschold described a second species, *P. stuckenbergi*, based on a specimen which had an elongate, narrow snout and lower jaw. This specimen was redescribed by Efremov (1933), who also described a third species, *P. watsoni*, of which ten skulls were available, all from the same locality. Efremov stated that *P. watsoni* had a narrower snout than *P. stuckenbergi*, and this is also shown in his figures of the skulls (Text-fig. 3D). (His figure of *P. watsoni* in dorsal view was later used by Romer (1947, fig. 28) as his illustration of the genus *Platyoposaurus*.) However, Efremov also figured the lower jaw of this specimen of *P. stuckenbergi*, and this has a degree of narrowing and elongation very similar to that of *P. watsoni*. Efremov also stated that he could not locate the position of the external nares of *Platyoposaurus*, even approximately – presumably because, like those of *Prionosuchus*, these were narrow slits located on the sides of the snout.

Bystrow (1935) also gave figures of the skull of *P. watsoni*, but showed this as having a much wider snout than that shown in either of Efremov's figures, and with dorsally-directed external nares quite unlike those of the other specimens. However, this was reconstructed from fragments in the Paleozoological Institute in Stockholm, and is unlikely to be more reliable than Efremov's series of more complete specimens. Konzhukova (1955) has given the most recent account of *P. stuckenbergi*, basing this on a new specimen which includes much of the post-cranial skeleton but which unfortunately lacks the snout. A complete skull of *Platyoposaurus*, identified as *P. watsoni*, in the Museum of Comparative Zoology, Harvard (MCZ 1750) shows a snout shape identical to that of Efremov's reconstruction of that species, with no trace of the external nares in dorsal view.

There is clearly some uncertainty over the proportions of the snout in these two species of *Platyoposaurus* and, in view of the variable crushing of the cavities in the snout of *Prionosuchus*, it seems very likely that only one species is really present in the Russian deposits. It also seems unlikely (though not impossible) that two similar piscivorous species could co-exist with one another in the same environment. *P. watsoni* (Efremov) is therefore considered to be a junior synonym of *P. stuckenbergi*.

There can nevertheless be no doubt that the snout of *Prionosuchus* is even more elongate than that of the Russian forms (Text-figs 3E, F), and that it represents a new taxon of archegosaur. It is, however, debatable whether the Brazilian form should be placed in a separate genus from *Platyoposaurus*, or should instead be regarded as merely another species of that genus. Until a complete skull of *Prionosuchus* is found, it is impossible to know whether its degree of morphological difference from *Platyoposaurus* suggests recognition at specific or at generic level. For the time being, therefore, there is insufficient evidence to justify an alteration in the present taxonomic position.

Prionosuchus appears to represent a continuation of the archegosaur trend towards an elongate, narrow snout, and this implies that it is more advanced than *Platyoposaurus* in this character. Price, in his original description of *Prionosuchus* (1948), stated that he believed it was a primitive platyoposaurid. He gave no reasons for this statement, but his discussion of the diagnostic features of *Prionosuchus* mentions five characters in which it differs from *Platyoposaurus*: the greater anterior prolongation of the nasals and premaxillae; the narrow, widely-separated internal nares; the narrow, laterally-placed external nares; the much greater number of denticles on the palate; and the very pronounced lateral-line canals. Barberena (1972) concurs with Price in regarding *Prionosuchus* as a primitive platyoposaurid, and quotes these same characters as evidence. However, the first two characters seem to be results of the great elongation of the snout, which is surely an advanced character. The multiplication of the palatal teeth also seems to be an advanced character, while the depth of the lateral-line canals is variable within *Prionosuchus*. There therefore appears to be no reason for regarding *Prionosuchus* as a primitive platyoposaurid, but several characters instead suggest that it is more advanced than *Platyoposaurus*.

Barberena and Daemon (1974) have described a long-snouted temnospondyl from the Permian Rio do Rasto Formation of the Parana Basin, southern Brazil. Though they at first ascribed this form to *Platyoposaurus*, later discovery of the more posterior parts of the skull has shown that it is probably related to the trematosaurs rather than to the archegosaurs (Barberena pers. comm. 1976), though such a late date would be surprising for a member of that group, and the specimen does not show the conspicuous parallel vomerine tooth-rows characteristic of the trematosaurs.

In his original description of *Prionosuchus*, Price (1948) suggested that the Pedra de Fogo Formation was of Early Permian age. This was mainly because he felt that the general nature of the sediments and fauna was very similar to that of the Early Permian Red Beds of Texas, in which he had collected earlier. In addition, Price pointed out that the Pedra de Fogo fauna contained ctenacanth, which were then unknown from deposits later than Early Permian age. However, Bendix-Almgreen and Mahl Zahn (1969) have since described a ctenacanth from the Kupferschiefer of Germany, which is of Late Permian age, even later than that of the *Platyoposaurus* specimens from Zone II of Russia. The other elements in the Pedra de Fogo Formation are of no use for dating purposes: xenacanth range from the Devonian to the Late Triassic (Patterson 1967), the dipnoan

fragments are too incomplete to allow of any identification even to family level, and *Brazilichthys* is isolated in a new family of actinopterygian fish. Though the fossil wood known as *Psaronius* is known only up to the Middle Permian of Europe, the Late Permian floras of Europe do not include petrification floras in which such wood would have been preserved. However, leaves of the *Pecopteris* type, considered to be those borne by *Psaronius*, have a much longer range in time (up to the Triassic), but the genus *Pecopteris* is so poorly defined that this range cannot be considered as reliable (W. G. Chaloner pers. comm.).

There is therefore little firm evidence on which to base an estimate of the age of the Pedra de Fogo Formation, other than that long-snouted archegosauroids are only known elsewhere from the Late Permian, which suggests a Late Permian age for the Formation. This in turn suggests that the Motuca Formation, which unconformably overlies the Pedra de Fogo Formation, is of Triassic age rather than Late Permian.

The re-assignment of the Pedra de Fogo Formation to the Late Permian is of additional palaeobiogeographical interest, in view of the fact that *Prionosuchus* had previously appeared to be one of the few tetrapods known outside Euramerica before the Late Permian. The realization of that fact provoked the suggestion (Cox 1974) that this was because Euramerica was still isolated from other continents until that time. However, it now appears that Euramerica had joined with Gondwana during the Carboniferous. Parrish *et al.* (1986) point out that all the occurrences of tetrapods prior to the Late Permian are found in equatorial to subequatorial palaeolatitudes, and that cool conditions for the Late Carboniferous to Early Permian are indicated by the distribution of coals, tillites and evaporites. They therefore suggest that climate was the principal cause of the absence of tetrapods from the higher southern palaeolatitudes of Gondwana until the Late Permian climatic improvement.

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It is sad to have to record that Dr Peter Hutchinson died in 1977, at the early age of 33, before this paper was completed. Its final completion took place during a year's sabbatical leave, and I am very grateful to the Principal of King's College London, for permission to take that leave, and to the Fulbright Commission for its generosity in providing a travel grant. I am also grateful to Dr Phil Hanawalt of the Department of Biological Sciences, Stanford University, California, for providing office and library facilities, and for his personal help and kindness.

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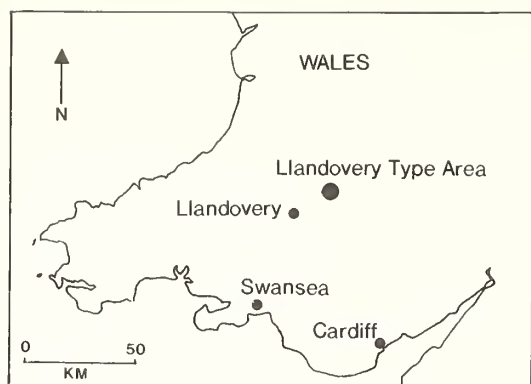
SILURIAN CRYPTOSPORES AND MIOSPORES FROM THE TYPE LLANDOVERY AREA, SOUTH-WEST WALES

by N. D. BURGESS

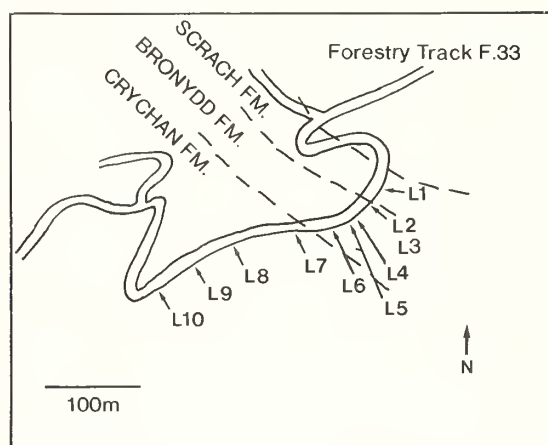
ABSTRACT. The oldest cryptospores and miospores have great significance in studies of the evolution of land plants: the former may represent the earliest direct evidence of such organisms and the latter may provide evidence for rhyniophytoid land plants as they have been recovered from the sporangia of *Cooksonia pertoni* Lang in the late Silurian. In the type Llandovery area, two distinct sporomorph assemblages are described from a composite section through uppermost Ordovician, Rhuddanian, Aeronian and basal Telychian strata. The older (latest Ordovician to late Aeronian) comprises eight genera and fourteen species of cryptospores (tetrads, pseudodyads, true dyads and monads). The younger (late Aeronian to Telychian) is dominated by smooth-walled trilete miospores of species of the genus *Ambitisporites*. Both assemblages have strong similarities to those described from similar horizons around the world. Specimens of *Ambitisporites dilutus* from the *sedgwickii* Graptolite Biozone of the Aeronian/Telychian type boundary section are the oldest known with unequivocal dating. They are used to define the base of the *Ambitisporites dilutus* – *A. avitus* Sporomorph Zone. Three new cryptospore genera (*Rimosotetras*, *Segestrespora* and *Velatitetras*) are erected and *Tetradraletes* is emended and synonymized with *Nodospora*. Six new cryptospore species (*Velatitetras laevigata*, *V. reticulata*, *V. rugulata*, *Rimosotetras problematica*, *Segestrespora laevigata* and *S. rugosa*), and two new varieties (*T. medenensis* vars *medenensis* and *parvus*) are described, and two combinations are made.

CURRENTLY sporomorphs provide the most convincing evidence for the existence of land plants in the late Ordovician and early Silurian (Gray 1985), the best being those with the greatest similarity to ones from living plants, or fossils of proven land-plants (Gray *et al.* 1982; Edwards *et al.* 1983; Gray 1985; Richardson 1985; Fanning *et al.* 1988). Spores in almost all such plants are produced in tetrads which separate on maturity to yield four trilete miospores. There are few records of trilete miospores in the Llandovery (Hoffmeister 1959; Cramer 1968, 1969; Pratt *et al.* 1978; Aldridge *et al.* 1979; Hill *et al.* 1985; Gray 1988; Richardson 1988). However, recent work has demonstrated the presence of permanently fused tetrads, dyads and monads, all of which can be enclosed within an envelope, in the late Ordovician and early Llandovery (e.g. Gray and Boucot 1971; Strother and Traverse 1979; Gray *et al.* 1982; Miller and Eames 1982; Gray 1985; Johnson 1985; Vavrdova 1982, 1984, 1988). As these unusually constructed cryptospores (*sensu* Richardson *et al.* 1984) may represent the oldest evidence of land-plants they have become important in the debate on the appearance and subsequent evolution of such organisms (Gray and Boucot 1977; Taylor 1982; Richardson 1985; Gray 1985, 1988).

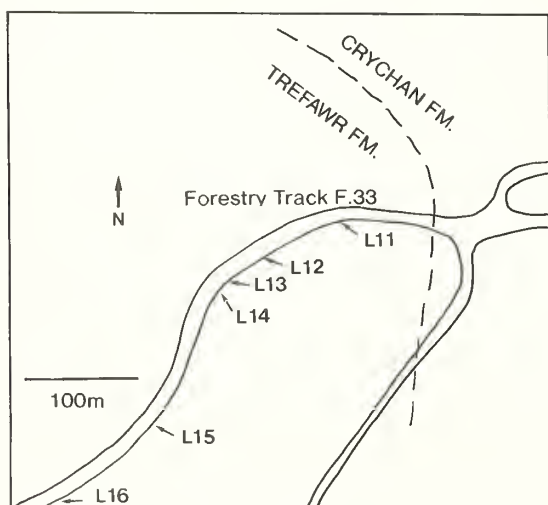
Despite their importance, few assemblages of Ordovician and Llandovery sporomorphs have been described from well-dated sections, or ones covering a long stratigraphic interval (Pratt *et al.* 1978; Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985; Richardson 1988). This has hindered interpretation of the biostratigraphic and evolutionary significance of the sporomorphs. This paper presents full descriptions and stratigraphic ranges for those cryptospores and trilete miospores recovered from a composite section through the uppermost Ordovician and the majority of the Llandovery Series in the type Llandovery area (Cocks *et al.* 1984).



TEXT-FIG. 1. Location of the type Llandovery area in southern Wales.

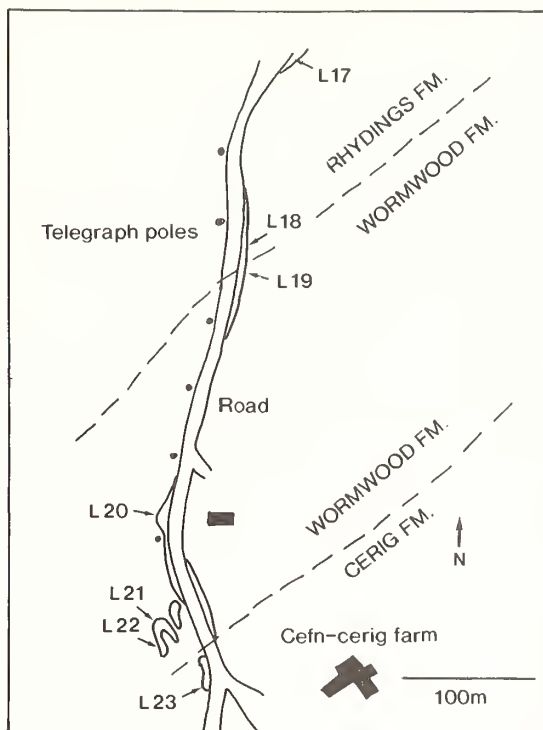


TEXT-FIG. 2. Locations of samples collected from the late Ordovician Scrach Formation to the early Llandovery Bronydd and Crychan formations in the type Llandovery area: Forestry track F.33, Crychan Forest near Llandovery (Ordnance survey map reference SO 84583964 at sample L1 = locality 24 of Cocks *et al.* 1984).



TEXT-FIG. 3. Locations of samples collected from the Rhuddanian/Aeronian type boundary section in the type Llandovery area: Forestry track F.33, Crychan Forest, near Llandovery (Ordnance survey map reference SO 83913960 at sample L11 = locality 38 of Cocks *et al.* 1984).

TEXT-FIG. 4. Locations of samples collected from the Aeronian/Teychian type boundary section in the type Llandovery area: roadside near Cefn Cerig farm, near Llandovery (Ordnance survey map reference SO 77543271 at sample L17 = locality 154 of Cocks *et al.* 1984).



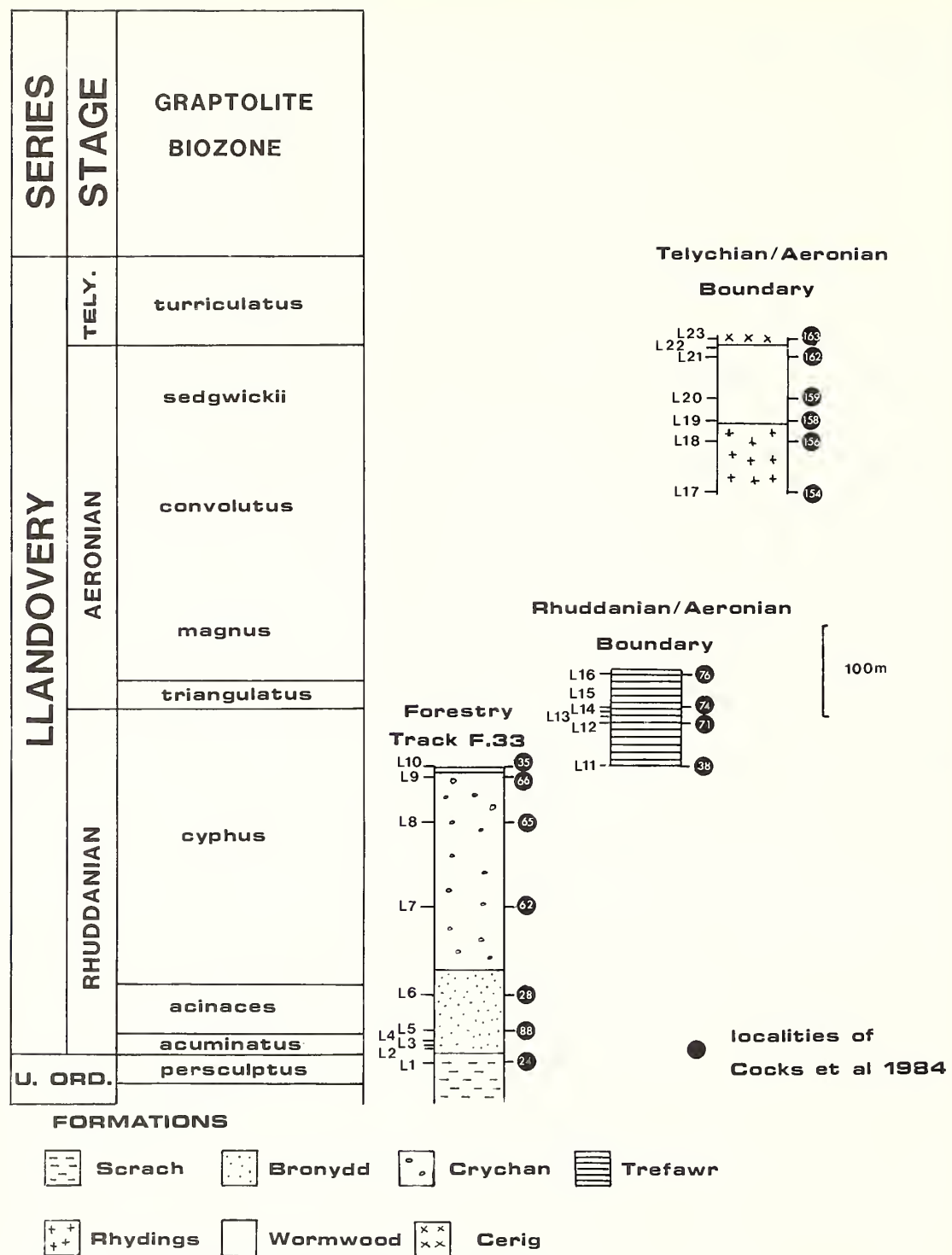
GEOLOGY, SAMPLING AND TECHNIQUE

The location of the type Llandovery area is presented in Text-figure 1. A single sample was collected from the uppermost Ordovician and twenty-two from the Llandovery Series. Sequences collected spanned the Ashgill/Rhuddanian boundary exposed along Forestry Track F. 33 next to the Afon Crychan river in Crychan Forest, c. 7 km north-east of Llandovery (Text-fig. 2), the Rhuddanian/Aeronian type boundary section (Text-fig. 3) and the Aeronian/Telychian type boundary section (Text-fig. 4) (Cocks *et al.* 1984). The top c. 100 m of the sequence in the type area were not sampled: this interval covers the *crispus* to *crenulatus* Graptolite Biozones. The stratigraphical framework of the samples is given in Text-figure 5.

The Llandovery sediments of the type area were deposited during a transgression which affected the whole of the Anglo-Welsh Basin (Cocks *et al.* 1984; Ziegler *et al.* 1968). As a consequence the samples collected during this study are from increasingly distal marine facies further up the section (Table 1). However, there may be slight shallowing event in the Wormwood Formation.

TABLE 1. Distribution of samples by geological formation with the ages and probable depositional environment.

Samples	Formation	Age	Probable depositional environment (Cocks <i>et al.</i> 1984)
L23	Cerig	early Telychian	Open marine shelf
L19-L22	Wormwood	late Aeronian	Open marine shelf
L17-L18	Rhydings	late Aeronian	Open marine shelf
L11-L16	Trefawr	early Aeronian	Open marine shelf
L7-L10	Crychan	late Rhuddanian	Open marine prograding delta lobe
L2-L6	Bronydd	early Rhuddanian	Mud-dominated marine shelf with storms
L1	Scrach	latest Ashgill	Shallow sub-tidal or even intertidal



TEXT-FIG. 5. Biostratigraphic and lithostratigraphic position of samples from the type Llandovery area, in relation to localities of Cocks *et al.* (1984).

Samples varied from dark mudstones in the Scrach and Bronydd formations through to muddy siltstones and silty mudstones for the remainder of the sequence. Palynomorphs were extracted using standard palynological methods (HCl then HF acids followed by sieving with 10 μm filter mesh and separation of the organic fraction using zinc bromide solution (S.G. 2.0)). Residues were oxidized in cold Schultze's solution for c. 48 hours. The sporomorphs remain dark, but poor preservation did not allow any further extension of the oxidation time. When this was attempted all the sporomorphs disintegrated. After oxidation, the acidic residues were neutralized with distilled water.

For light microscope observation, measured volumes of material were strewn on to glass coverslips, dried, and the coverslips attached to glass slides with 'Elvacite' plastic mounting medium.

Photomicrographs were taken on FP4 film using a Zeiss photomicroscope III (no. 2562) housed in the Palynology Laboratory of the British Museum (Natural History) (BM(NH)), and using Nomarski differential interference contrast with an orange filter to reduce contrast between the palynomorphs and the background.

SYSTEMATIC PALAEONTOLOGY

Preamble. Sporomorphs are described, where possible, using the standard terminology of Grebe (1971). Specimen dimensions are presented as the minimum and maximum of the range, with the mean in brackets. Stratigraphic range refers to range within the type Llandovery area only. The stratigraphical occurrence of taxa is shown in Text-figure 7 and the stratigraphical distribution and correlation of the samples in Text-figure 5.

Specimens are located by means of standard England Finder and microscope stage co-ordinates taken from the Zeiss photomicroscope III (no. 2562) housed in the Palynology Laboratory at the BM(NH). All figured specimens are also ringed with a red indelible pen. Slides and stubs containing figured specimens (prefixed FM) are stored in the Palynology collection at the BM(NH).

Anteturma CRYPTOSPORITES Richardson *et al.*, 1984

1. *Cryptospore* tetrads

This group comprises tetrads and dyads which are not found separated into individual components spores and which are believed to be 'permanently' fused. They may also be enclosed within a sculptured or non-sculptured envelope.

Genus TETRAHEDRALETES Strother and Traverse, 1979 emend.

Type species. *Tetrahedraletes medinensis* Strother and Traverse, 1979 from the Tuscarora Formation, Pennsylvania, USA.

Emended diagnosis. Permanent tetrahedral cryptospore tetrads, permanently fused. Tetrads sub-circular to circular in outline and composed of four laevigate, crassitate, sub-triangular 'spores'. Crassitudes of individual 'spores' $\pm$ equatorial, fused or discrete. Distal 'spore' walls tend to invaginate, but can remain inflated.

Discussion. *Tetrahedraletes* Strother and Traverse was erected to encompass 'tetrads of inaperturate, sub-triangular spores or spore-like palynomorphs arranged in tightly adhering tetrahedron configuration, with the spore walls collapsed towards the centre' (Strother and Traverse 1979, p. 8). *Nodospora*, a similar genus, was defined for 'tetrads of inaperturate spores or spore-like palynomorphs, spherical to sub-spherical in outline, which are arranged in a cross configuration' (Strother and Traverse (1979, p. 10). Data collected here and in other recent publications (e.g. Gray *et al.* 1985; 1986; Gray 1985; 1988) indicate that the type specimens of *Tetrahedraletes* (*T. medinensis*) and *Nodospora* (*N. burnhamensis*) should be placed in synonymy, the two taxa representing different compressional morphologies of otherwise identical tetrads. Hence, in this publication all such tetrads are placed in *Tetrahedraletes* and the diagnosis of this genus emended accordingly.

Tetrahedraletes medinensis Strother and Traverse, 1979 emend.

This species has been subdivided into two varieties based on size because the original specimens (Strother and Traverse 1979) are much larger than those recorded from the late Ordovician and early Llandovery (e.g. Gray 1988).

Tetrahedraletes medinensis Strother and Traverse, 1979 var. *medinensis* var. nov.

Holotype and type locality. Strother and Traverse, 1979, pl. 1, fig. 5: Harvard Paleobotanical Collections no. 60289, slide no. 75-4/A3, location on slide 34.8 mm × 107.9 mm, reference point 13.3 mm × 109.2 mm. Samples 75-4, Tuscarora Formation; Section – Mann Narrows along route 322, north-west of Burnham, Mifflin County, Pennsylvania, USA.

Description. As for Strother and Traverse (1979).

Comparison. Cryptospores of *Tetrahedraletes medinensis* var. *parvus* var. nov. are < 35 µm in diameter, but otherwise identical.

Remarks. This variety of *T. medenensis* is common in the basal Wenlock (Burgess and Richardson 1991) but is not known from the uppermost Ordovician or early Llandovery of the type area where the following variety is found (also see Gray 1988).

Tetrahedraletes medinensis var. *parvus* var. nov.

Plate 1, figs 1–4

1985 *Tetrahedraletes* cf. *T. medinensis* Gray, fig. 5 F–H.

EXPLANATION OF PLATE 1

All figures × 1000 unless stated otherwise.

Figs 1–4. *Tetrahedraletes medinensis* Strother and Traverse, 1979 emend. var. *parvus* var. nov. 1, FM 187, holotype (slide Llan 8B/12, 178 1170; E.F. no: S47/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, × 2000. 2, FM 188 (slide Llan 8B/8, 061 1283; E.F. no: F58/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 3, FM 92 (slide Llan 5/2, 130 960; E.F. no: N26/1), sample L16, Trefawr Formation, *triangulatus* Graptolite Biozone. 4, FM 189 (slide Llan 1/1, 112 1204; E.F. no: K50/4), sample L11, Trefawr Formation, *cyphus* Graptolite Biozone.

Figs 5 and 6. *Velatitetras laevigata* gen. et sp. nov. 5, FM 190 (slide Llan 8B/11, 179 1294; E.F. no: S59/S60), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 6, FM 191, holotype (slide Llan 2/1, 050 1215; E.F. no: E51/4, sample L12, Trefawr Formation, *cyphus* Graptolite Biozone.

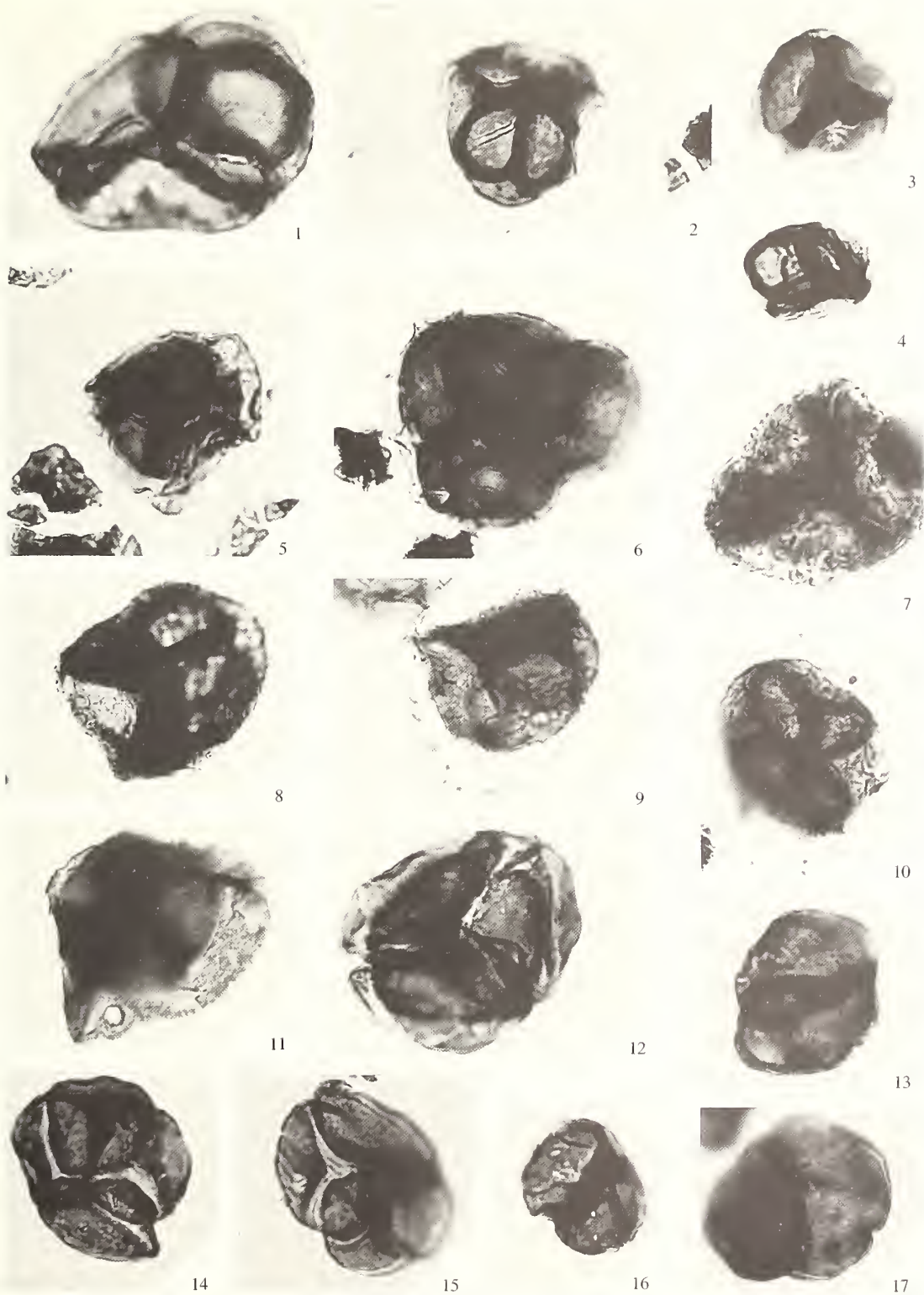
Figs 7–9. *Velatitetras reticulata* gen. et sp. nov. 7, FM 91 (slide Llan 1/2, 232 1110; E.F. no: Y41/2), sample L11, Trefawr Formation, *cyphus* Graptolite Biozone. 8, FM 197 holotype (slide Llan 8B/9, 128 1253; E.F. no: N55/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 9, FM 192 (slide Llan 8B/8, 106 1304; E.F. no: K60/61/L60/61), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 10. *Velatitetras rugulata* gen. et sp. nov. FM 194, holotype (slide Llan 8B/12, 128 1220; E.F. no: M52/3/M51/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 11. *Velatitetras* sp. A. FM 195 (slide Llan 8B/15, 118 1277; E.F. no: M58/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 12, 14, 15. *Rimosotetras problematica* gen. et sp. nov. 12, FM 196 (slide Llan 8B/12, 240 1080; E.F. no: Y38/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 14, FM 198, holotype (slide Llan 8B/6, 138 1228; E.F. no: 053/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 15, FM 199 (slide Llan 8B/8, 147 1089; E.F. no: P38/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 13, 16, 17. *Pseudodyadospora* cf. *laevigata* Johnson, 1985. 13, FM 197 (slide Llan 8B/26, 035 1250; E.F. no: C55/1/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 16, FM 200 (slide Llan 8B/22, 226 1112; E.F. no: X41/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 17, FM 201 (slide Llan 8B/12, 240 1095; E.F. no: Y39/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.



BURGESS, Llandovery sporomorphs

- 1985 *Tetrahedraletes* cf. *T. medinensis* Gray *et al.*, p. 524, fig. 5 F–H.
 1986 *Tetrahedraletes* cf. *T. medinensis* Gray *et al.*, p. 451, fig. 7, items 1–7.
 1988 'Smooth walled tetrads', Gray, p. 355, pl. 1, figs 1 and 5.
 1988 *Tetrahedraletes* sp., Richardson, pl. 19, fig. 1.

Holotype and type locality. FM 187, Pl. 1, fig. 1, slide Llan 8B/12, 178 1170, E.F. no: S47/1, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

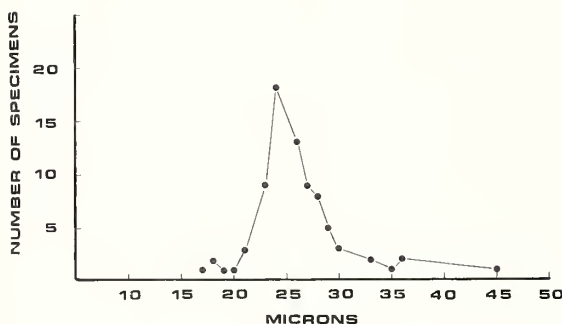
Paratypes. FM 188, Pl. 1, fig. 2, slide Llan 8B/8, 061 1283, samples L5; Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone; FM92, Pl. 1, fig. 3, slide Llan 5/2, 130 0960, sample L20, Aeronian/Telychian boundary section, Wormwood Formation, *sedgwickii* Graptolite Biozone; FM 189, Pl. 1, fig. 4, slide Llan 1/1, 020 1204, sample L11, Rhuddanian/Aeronian boundary section, Trefawr Formation, *cyphus* Graptolite Biozone.

Derivation of name. Latin *parvus*, small.

Diagnosis. A variety of *Tetrahedraletes medinensis* < 35 μm in diameter with low, narrow, rounded and unfused equatorial crassitudes.

Description. Laevigate oblique tetrads, sub-circular to circular in outline and preserved in a variety of compressional morphologies depending on the degree of rotation of the tetrad from an apical view prior to compression. Individual 'spores' laevigate, amb sub-circular to sub-triangular, joined by unfused equatorial crassitudes 1–5 μm wide. Proximal surface not observed. Distal exine 1–2 μm thick and invaginated in most specimens.

Dimensions. Tetrads 19 (26) 30 μm in diameter (150 specimens measured, see Text-figure 6 for range of measurements).



TEXT-FIG. 6. Size frequency distribution of a hundred *Tetrahedraletes medinensis* var. *parvus* tetrads from sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Biostratigraphical range. Latest Ordovician (*persculptus* Graptolite Biozone), to early Telychian (*turriculatus* Graptolite Biozone; Text-fig. 7).

Comparisons. *Tetrahedraletes medinensis* var. *medinensis* is larger (> 35 μm). Specimens described as *Tetrahedraletes* cf. *T. medinensis* (Gray 1988) from various sections spanning the Ordovician/Silurian boundary around the world have essentially identical measurements to those described above.

Remarks. Gray (1988) has presented data showing that tetrads gradually increase in size over the Ordovician/Silurian boundary and states that this increase continues through the Llandovery. In the Anglo-Welsh Basin, *T. medinensis* var. *parvus* var. nov. is the dominant variety in the latest Ordovician and early Llandovery, whereas *T. medinensis* var. *medinensis* Strother and Traverse, 1979 dominates in the basal Wenlock (Burgess and Richardson 1991).

Genus VELATITETRAS gen. nov.

Type species. Velatitetras laevigata sp. nov.

This genus is erected to accommodate tightly adherent cryptospore tetrads enclosed within an envelope. Some specimens of *Nodospora* Strother and Traverse are believed to possess an envelope (e.g. *N. retimembrana*). However, because the type species of *Nodospora* (*N. buruhamensis*) lacks an envelope and is considered synonymous with the type species of *Tetrahedraletes* (*T. medinensis*) the genus *Nodospora* cannot be used for enveloped forms. *Stegambiquadrella* Johnson was erected for palynomorphs with four loosely-attached inaperturate vesicles enclosed within an envelope. This genus cannot be used to accommodate tightly-adherent tetrahedral tetrads enclosed within an envelope.

Derivation of name. Latin *velatus*, covered; *tetras*, tetrad.

Diagnosis. Obligate cryptospore tetrads composed of tightly-adherent laevigate sub-triangular to sub-circular 'spores' with low and rounded $\pm$ fused equatorial crassitudes. Tetrads enclosed within a closely adherent to completely separated, $\pm$ ornamented envelope; when envelope tightly-addressed any ornamentation passes over 'spore' contacts uninterrupted.

Velatitetras laevigata sp. nov.

Plate 1, figs 5 and 6

1985 'Obligate tetrad with smooth perispore', Gray, p. 177, pl. 1, figs 2 and 3.

1988 'Spore tetrad with smooth or possibly degraded reticulate envelope', Gray, p. 355, pl. 1, fig. 3.

1988 *Nodospora* sp. B, Richardson, p. 94.

Holotype and type locality. FM 191, Pl. 1, fig. 6, slide Llan 2/1, 050 1215, E.F. no: E51.4, sample L12 (Text-fig. 3), Rhuddanian/Aeronian type boundary section, Trefawr Formation, *cyphus* Graptolite Biozone, late Rhuddanian.

Paratype. FM 190, Pl. 1, fig. 5, slide Llan 8B/11, 179 1294, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *laevigatus*, smooth.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within a thin, laevigate and often folded envelope.

Description. Obligate tetrads, sub-circular to circular in outline, totally enclosed within an envelope. Tetrads composed of laevigate, sub-triangular 'spores' with unfused, low and rounded equatorial crassitudes 1–3 μ m wide; distal polar exine c. 1 μ m thick. Envelope laevigate, diaphanous, folded and < 1 μ m thick; varies from completely separated, to closely adpressed to tetrad.

Dimensions. Enclosed tetrads 21 (27) 34 μ m in diameter (22 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone), to late Rhuddanian (*cyphus* Graptolite Biozone; Text-fig. 7).

Comparisons. Gray (1985, pl. 1, figs 2 and 3; 1988, pl. 1, fig. 3), illustrated small (c. 25 μ m) and essentially identical tetrads enclosed within smooth envelopes from the Late Ordovician of America.

Velatitetras reticulata sp. nov.

Plate 1, figs 7–9.

1985 Obligate tetrad with 'reticulate perispore', Gray, p. 177, pl. 1, figs 4–9; pl. 2, fig. 17.

1988 Obligate tetrad with 'reticulate envelope', Gray, p. 355, pl. 1, figs 2, 4, 6.

Holotype and type locality. FM 192, Pl. 1, fig. 8, slide Llan 8B/9, 128 1253, E.F. no: N55/2, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Paratypes. FM 91, Pl. 1, fig. 7, slide Llan 1/2, 232 1110, sample L11, Rhuddanian/Aeronian boundary section, Trefawr Formation, *cyphus* Graptolite Biozone; FM 193, Pl. 1, fig. 9, slide Llan 8B/8, 106 1304, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *reticulatus*, netted, marked with a network – refers to arrangement of muri on envelope.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within an envelope ornamented with muri forming a reticulum with small lumen.

Description. Obligate tetrads sub-circular to circular in outline, totally enclosed within an envelope. Tetrads composed of laevigate, inaperturate, sub-triangular to sub-circular 'spores' with unfused equatorial crassitudes 1–3 μm wide; exine at distal pole *c.* 1 μm thick. Envelope closely adpressed to widely separated from enclosed tetrad and ornamented with low (*c.* 1 μm), rounded muri 0.5 (1) 1.5 μm wide, which usually form an ill defined reticulum 1–3.5 μm in maximum diameter, although this may be of regular size and distribution over the envelope.

Dimensions. Enclosed tetrads 22 (27) 35 μm in diameter (14 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Aeronian (*sedgwickii* Graptolite Biozone; Text-fig. 7).

Comparisons. Comparable specimens have been described by Gray (1985, pl. 1, figs 4–9; pl. 2, fig. 17) and Gray (1988, pl. 1, figs 2, 4, 6) from the Ashgill of the USA. *Velatitetras rugulata* sp. nov. is of similar size, but has sinuous rugulae on its envelope. '*Nodospora*' *retimembrana* Miller and Eames, 1982 is much larger (34–60 μm) and the reticulum on the envelope is both larger and more regularly arranged.

Velatitetras rugulata sp. nov.

Plate 1, fig. 10

Holotype and type locality. FM 194, Pl. 1, fig. 10, slide Llan 8B/12, 128 1220, E.F. no: M52/3/M51/4, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Derivation of name. Latin *rugulatus*, refers to rugose ornamentation on envelope.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within an envelope ornamented with sinuous to convolute and anastomosing rugulae.

Description. Obligate tetrads sub-circular to circular in outline, totally enclosed within an envelope. Tetrad composed of laevigate, inaperturate, sub-triangular 'spores' with low and rounded unfused equatorial crassitudes 1–3 μm wide; exine at distal pole *c.* 1 μm thick. Envelope closely adpressed to completely separated from enclosed tetrad and ornamented with low, rounded rugulae 0.5–1 μm wide, < 1 μm high and 1.5 (2.5) 3 μm apart; rugulae are closely spaced, slightly sinuous to convolute and occasionally anastomosing.

Dimensions. Enclosed tetrads 24 (28.5) 33 μm in diameter (13 specimens measured).

Biostratigraphic range. Early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Velatitetras reticulata* sp. nov. is of similar size but the muri on its envelope form a reticulum. '*Nodospora*' *rugosa* Strother and Traverse, 1979, *Nodospora* sp. A Richardson 1988, and *N. cf. rugosa* Miller and Eames 1982 are much larger ($> 43 \mu\text{m}$).

Velatitetras sp. A

Plate 1, fig. 11

?1988 *Nodospora* sp. E, Richardson, p. 94.

Figured specimen. FM 195, Pl. 1, fig. 11, slide Llan 8B/15, 118 1277, E.F. no: M58/1, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Description. Obligate tetrad sub-circular in outline, totally enclosed within an envelope. Tetrad composed of laevigate, inaperturate, sub-triangular 'spores' with low and rounded crassitudes $1\text{--}3 \mu\text{m}$ wide. Envelope separated from tetrad and ornamented with closely packed grana.

Dimensions. 1 specimen with enclosed tetrad of $25 \mu\text{m}$ diameter.

Biostratigraphic range. Bronydd Formation, *acinaces* Graptolite Biozone (Text-fig. 7).

Comparisons. The granulate ornament on the envelope separates this tetrad from all other specimens. *Segestrespora* sp. A has a similarly ornamented envelope surrounding a pseudodyad.

Genus RIMOSOTETRAS gen. nov.

Type species. *Rimosotetras problematica* sp. nov.

Derivation of name. Latin *rimosus*, cracked.

Diagnosis. Adherent, but usually partially separating, tetrahedral tetrads composed of alete, laevigate, sub-triangular to circular, $\pm$ crassitate spores or spore-like units.

Remarks. In *Tetrahedraletes* Strother and Traverse, 1979 emend. the spores comprising the tetrad are much more tightly adherent. Tetrads of *Ambitisporites* Hoffmeister, 1959 separate more readily and produce miospores with obvious trilete marks.

Rimosotetras problematica sp. nov.

Plate 1, figs 12, 14, 15

1971 'Spore tetrad', Gray and Boucot, fig. 1(g).

1985 'Loose tetrads', Richardson, p. 29, pl. 15, figs 5 and 6.

1988 *Nodospora burnhamensis* 'loose tetrad', Richardson, pl. 19, figs 11 and 12.

Holotype and type locality. FM 198, Pl. 1, fig. 14, slide Llan 8B/6, 138 1228, E.F. no: 053/1, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Paratypes. FM 196, Pl. 1, fig. 12, slide Llan 8B/12, 240 1080; FM 199, Pl. 1, fig. 15, slide Llan 8B/8, 147 1089, both sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *problematicus*, problematic; refers to problematic nature of these sporomorphs which are similar to permanently fused cryptospore tetrads, but which appear to separate into alete 'spores', in other ways similar to trilete miospores.

Diagnosis. A *Rimosotetras* with sub-triangular 'spores' possessing rounded, non-projecting, equatorial crassitudes.

Description. Cryptospore tetrads sub-circular to circular in outline and preserved in a variety of compressional morphologies reflecting rotation of tetrad from an apical view prior to compression. Tetrads composed of loosely attached, frequently partially separated, laevigate, alete or indistinctly trilete, sub-triangular to sub-circular 'spores' with narrow and rounded equatorial crassitudes 0.75 (1.5) 2.5 μm wide. Distal exine convex c. 1 μm thick, usually inflated, but can be invaginated. Proximal surface lacks sutures typical of trilete miospores, although specimens may have a crack or split at the position of a trilete mark indicating a weakness of the exine.

Dimensions. Tetrads 23 (28) 42 μm in diameter (38 specimens measured). Individual spores 15 (22) 35 μm in diameter (67 measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Rhuddanian (*cyphus* Graptolite Biozone) (Text-fig. 7).

Comparisons. Comparable 'loose' tetrads have been recorded in the Rhuddanian of Libya by Richardson (in Hill *et al.* 1985, p. 29) and Richardson (1988). The spore tetrad from North America drawn by Gray and Boucot (1971, fig. 1(g)) also appears similar.

2. *Cryptospore dyads*

This group encompasses permanently fused dyads (pseudodyads) which may be enclosed within a variously ornamented envelope and dyads which readily separate into two alete spores (true dyads).

Genus PSEUDODYADOSPORA Johnson, 1985

Type species. *Pseudodyadospora laevigata* Johnson, 1985.

Pseudodyadospora cf. *laevigata* Johnson, 1985

Plate 1, figs 13, 16, 17

Figured specimens. FM 197, Pl. 1, fig. 13, slide Llan 8B/26, 035 1250; FM 200, Pl. 1, fig. 16, slide Llan 8B/22, 226 1112; FM 201, Pl. 1, fig. 17, slide Llan 8B/12, 240 1095, all specimens sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaes* Graptolite Biozone.

Description. Pseudodyads elliptical to sub-circular or rarely circular in outline. 'Spores' of pseudodyad joined by a single encircling darkened band 1 (2) 3 μm wide providing no evidence for 'spore' separation. 'Spores' are of unequal size in 62% of the specimens, laevigate, and usually distally convex, although they can be invaginated. Exine often folded and 0.5–1 μm thick at distal pole.

Dimensions. Pseudodyads 22 (26) 42 μm long and 16 (22) 28 μm wide at equator (50 specimens measured). Length to width ratio = 1.3.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Aeronian (*sedgwickii* Graptolite Biozone; Text-fig. 7).

Comparisons. *Pseudodyadospora laevigata* Johnson, 1985 is similar in outline, the variable size of the 'spores' and the fused suture between the 'spores', but is somewhat larger (41 (52) 60 μm long), although there is some overlap in the sizes. Dyads in *Segestrespora* gen. nov. possess an envelope surrounding an otherwise similar pseudodyad. Dyads of the genus *Dyadospora* Strother and Traverse, 1979 have well developed lines of separation between the equally sized spores, and are generally seen partially separated into two alete sporomorphs (Burgess and Richardson 1991).

Genus *SEGESTRESPORA* gen. nov.

Type species. Segestrespora (Dyadospora) membranifera (Johnson) comb. nov.

Derivation of name. Latin *segestre*, covering or wrapper.

Diagnosis. Bipolar, laevigate and permanently fused pseudodyads, divided by a single central to slightly off-centred thickened encircling band, and totally enclosed within a closely adherent to completely separated envelope which either lacks ornamentation, or has apiculi, muri, rugulae or verrucae.

Remarks. In some specimens an envelope can not be easily seen. However, if any sculpture passes over the 'spore' contact uninterrupted, then an envelope is assumed to be present and specimens are assigned to *Segestrespora*.

Comparisons. The genus *Pseudodyadospora* Johnson is for obligate pseudodyads with only one wall-layer, which can be sculptured. In *Dyadospora* Strother and Traverse, the dyads lack an envelope and are readily separated into two laevigate alete spores.

Segestrespora (Dyadospora) membranifera (Johnson, 1985) comb. nov.

Plate 2, figs 2–5

1985 *Dyadospora membranifera* Johnson [*partim*], p. 336, pl. 7, figs 1–3, 5, 6, *non* pl. 7, fig. 7.

1988 *Pseudodyadospora* cf. *Dyadospora membranifera*, Richardson, p. 94, pl. 15, figs 1 and 2.

Holotype and type locality. Johnson, 1985, pl. 7, figs 1–3: sample TMH81-11-26, location EF D35-4; c. 75 m from base of Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m above US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimens. FM 203, Pl. 2, fig. 2, slide Llan 8B/7, 198 1020; FM 204, Pl. 2, fig. 3, slide Llan 8B/7, 220 2100; FM 205, Pl. 2, fig. 3, slide Llan 8B/11, 240 1170; FM 206, Pl. 2, fig. 5, slide Llan 8B/10, 130 1150, all sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Diagnosis. A *Segestrespora* where the envelope is ornamented with narrow muri which form a low, regular to irregularly sized and shaped reticulum.

Description. Pseudodyads elliptical to sub-circular in lateral view and totally enclosed within an envelope. Individual 'spores' of pseudodyad convex in lateral compression. Exine c. 1 μm thick with rare folds. A single darkened, possibly thickened, encircling band 1–2 μm wide joins the 'spores' which are anisomorphic in c. 75% of the specimens. The envelope is diaphanous and may be tightly adherent to the pseudodyad and difficult to resolve, or completely separated. Envelope is ornamented with muri, 0.5–1 μm wide and c. 0.5 μm high, which form a regularly to irregularly sized and shaped reticulum with lumen 1.5 (2) 3 μm in diameter.

Dimensions. Pseudodyads 25 (29) 31 μm long, 18 (20) 22 μm wide at equator (12 specimens). Length to width ratio = 1.4.

Biostratigraphic range. Late Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. Those specimens of '*Dyadospora membranifera*' Johnson, 1985 which possessed a reticulate envelope are members of this species, but those with a laevigate envelope are transferred to another species (see below). Specimens referred to *Pseudodyadospora* cf. *Dyadospora membranifera* by Richardson, 1988 are also members of this species. When specimens of *Segestrespora membranifera* have lost their membrane they are placed in *Pseudodyadospora laevigata* Johnson, 1985.

Segestrespora laevigata sp. nov.

Plate 2, fig. 1

- ?1982 *Dyadospora murusdensa* with 'membrane', Miller and Eames, p. 248.
 1985 '*Dyadospora membranifera*' Johnson, [partim], p. 336, pl. 7, fig. 7, non pl. 7, figs 1-3, 5, 6.
 ?1985 *Dyadospora murusdensa* 'with diaphanous sheath', Richardson in Hill *et al.*, p. 29.

Holotype. Johnson, 1985, pl. 7, fig. 7, Sample TMH81-8, c. 125 m above the base of the Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m about US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimen. FM 202, Pl. 2, fig. 1, slide Llan 8B/2, 103 1294, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *laevigatus*, smooth.

Diagnosis. A *Segestrespora* with a thin, folded and laevigate envelope.

Description. Pseudodyads elliptical to sub-circular in lateral view and totally enclosed within an envelope. Individual 'spores' of pseudodyad laevigate, distally convex in lateral compression, occasionally folded with walls c. 1 μ m thick. A single darkened encircling band 1–2 μ m wide joins 'spores' which are anisomorphic in c. 25% of observed specimens. Envelope is laevigate, < 1 μ m thick, often highly folded, and varies from being closely adpressed to the dyad and difficult to resolve, to completely separated.

Dimensions. Pseudodyads 26 (29) 41 μ m long, 17 (23) 31 μ m wide at equator (20 specimens measured). Length to width ratio = 1.3.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Segestrespora membranifera* comb. nov. has reticulate ornamentation on its envelope and *S. rugosa* comb. nov. has rugulate ornamentation. One of the specimens of '*Dyadospora membranifera*' Johnson possessed a smooth envelope (pl. 7, fig. 7) and this specimen is included in this new species. Other possible records of *S. laevigata*, all from the Rhuddanian, are: Miller and Eames (1982), who stated (p. 248) that membranes were occasionally found around '*Dyadospora murusdensa*'; Strother and Traverse (1979, p. 7) who recovered 'membrane enclosed bilaterally symmetrical opaque bodies'; and Richardson in Hill *et al.* (1985), who recorded 'diaphanous sheaths' (p. 29) around '*Dyadospora murusdensa*'.

Segestrespora (Pseudodyadospora) rugosa (Johnson, 1985) comb. nov.

Plate 2, figs 7–9

- 1985 *Pseudodyadospora rugosa* Johnson, p. 337, pl. VIII, figs 2–6.
 1988 *Pseudodyadospora* sp. C, Richardson, p. 95.

Holotype and type locality. Johnson, 1985, pl. 8, fig. 5, slide TMH81-3-27, location EF M39-4, c. 175 m above the base of the Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m above US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimens. FM 208, Pl. 2, fig. 7, slide Llan 8B/11, 077 1214; FM 209, Pl. 2, fig. 8, slide Llan 8B/6, 055 1125; FM 210, Pl. 2, fig. 9, slide Llan 8B/2, 086 1234; all sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Diagnosis. A *Segestrespora* with an envelope ornamented with regularly sinuous and closely spaced rugulae.

Description. Pseudodyads sub-circular to elliptical in lateral view, and totally enclosed within an envelope. Individual 'spores' of pseudodyad distally convex with a laevigate and occasionally folded wall *c.* 1 μ m thick. A single darkened and possibly thickened encircling band, 1–2 μ m wide, joins the 'spores' which are anisomorphic in *c.* 33% of the specimens. The envelope is tightly adpressed to completely separated from pseudodyad and ornamented with closely spaced, regularly sinuous, rugulae 0.5 (1) 1.5 μ m wide, < 1 μ m high and 0.5–1 μ m apart.

Dimensions. Pseudodyads 27 (29) 31 μ m long, 15 (20) 23 μ m wide at equator (12 specimens measured). Length to width ratio = 1.4.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Pseudodyadospora* sp. C Richardson, 1988 appears identical to these spores. *Pseudodyadospora rugosa* Johnson, 1985 is similarly ornamented, but Johnson (1985, p. 337) made no mention of whether the rugulae were on an envelope or the dyad wall. However, Johnson now believes (pers. comm. 1986) that there is a closely adherent envelope surrounding her pseudodyads. The envelope surrounding *Velatitetras rugulata* sp. nov. is similarly sculptured, but encloses a cryptospore tetrad.

EXPLANATION OF PLATE 2

All figures $\times 1000$ unless stated otherwise.

Fig. 1. *Segestrespora laevigata* gen. et sp. nov. FM 202 (slide Llan 8B/2, co-ord 103 1294; E.F. no: K59/2/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 2–5. *Segestrespora membranifera* (Johnson, 1985) comb. nov. 2, FM 203 (slide Llan 8B/7, co-ord 198 1020; E.F. no: T31/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, $\times 2000$. 3, FM 204 (slide 8B/7, co-ord 220 2100; E.F. no: W50/3/W49/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, $\times 2000$. 4, FM 205 (slide Llan 8/11, co-ord 240 1170; E.F. no: Y47/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, $\times 2000$. 5, FM 206 (slide Llan 8B/10, co-ord 130 1150; E.F. no: N45/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 6. *Segestrespora* sp.A. FM 207 (slide Llan 7B/4, co-ord 100 1015; E.F. no: K30/2), sample L1, Scrach Formation, *persculptus* Graptolite Biozone.

Figs 7–9. *Segestrespora rugosa* gen. et sp. nov. 7, FM 208 (slide Llan 8B/11, co-ord 077 1214; E.F. no: G51/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, $\times 2000$. 8, FM 209 (Llan 8B/6, co-ord 055 1125; E.F. no: E42/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 9, FM 210 (slide Llan 8B/2, co-ord 086 1234; E.F. no: H53/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 10. *Dyadospora murusattenuata* Strother and Traverse, 1979. FM 211 (slide Llan 8B/22, 138 1350; E.F. no: N65/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

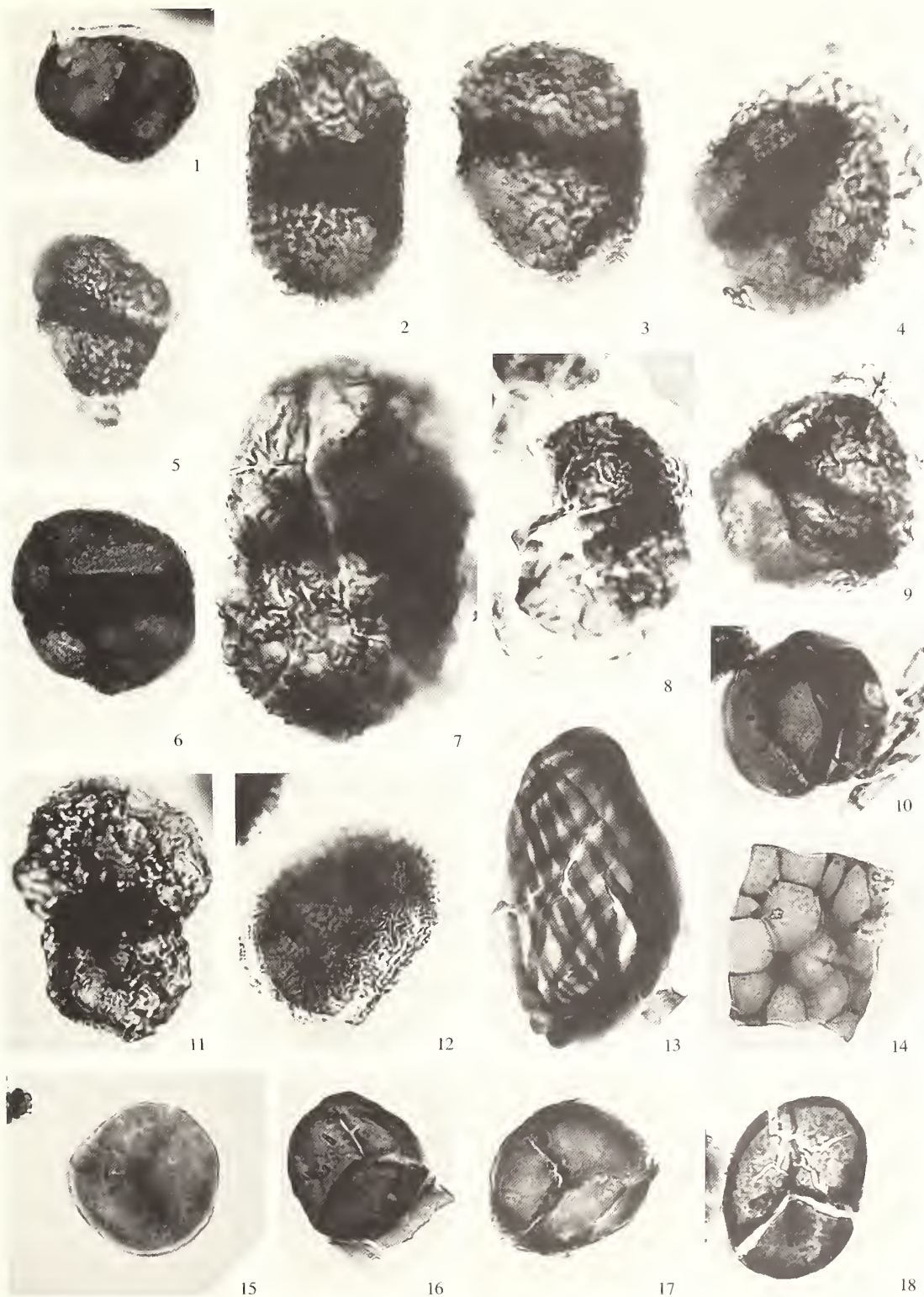
Figs 11 and 12. *Rugosphaera* cf. *R. cerebra* Miller and Eames, 1982. 11, FM 212 (slide Llan 8B/8, co-ord 110 1300; E.F. no: K60/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 12, FM 213 (slide Llan 8B/24, co-ord 101 1080; E.F. no: K37/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 13. *Strophomorpha ovata* Miller and Eames, 1982. FM 214 (slide Llan 3B/3, co-ord 035 1090; E.F. no: B39/1/2), sample L8, Crychan Formation, *cyphus* Graptolite Biozone.

Fig. 14. *Nematothallus* cuticle (see Edwards 1986). FM 219 (slide Llan 6/2, 237 1250; E.F. no: Y55/1), sample L21, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Fig. 15. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. FM 95 (slide Llan 6/2, co-ord 071 1160; E.F. no: G47/3), sample L21, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Figs 16–18. *Ambitisporites?* *vavrdovii* Richardson, 1988. 16, FM 216 (Llan 7B/6, 090 1180; E.F. no: J48), sample L1, Scrach Formation, *persculptus* Graptolite Biozone. 17, FM 217 (slide Llan 8B/6, 138 1225; E.F. no: P53/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 18, FM 218 (slide Llan 3B/1, 130 1296; E.F. no: N59/N60), sample L8, Crychan Formation, *cyphus* Graptolite Biozone.



BURGESS, Llandovery sporomorphs

Segestrespora sp. A

Plate 2, fig. 6

Figured specimen. FM 207, Pl. 2, fig. 6, slide Llan 7B/4, 100 1015, sample L1, Forestry Track F.33, Scrach Formation, *persculptus* Graptolite Biozone, latest Ordovician.

Description. Pseudodyads sub-circular to elliptical in equatorial view, and totally enclosed within an envelope. Individual 'spores' of pseudodyad distally convex, with a laevigate, occasionally folded wall *c.* 1 μm thick. A single, darkened and possibly thickened encircling band, 1–2 μm wide, joins 'spores' which are anisomorphic in *c.* 33 % of the specimens. The envelope varies from closely adpressed to the pseudodyad to completely separated from it, and is ornamented with regularly distributed and closely spaced grana < 0.5 μm high and wide and *c.* 0.5 μm apart.

Dimensions. Pseudodyads 29 (30.5) 35 μm long, 26 (27) 29 μm wide at equator (3 specimens only). Length to width ratio = 1.2.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone), to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparison. *Velatitetras* sp. A has a similarly ornamented envelope surrounding a cryptospore tetrad.

Genus DYADOSPORA Strother and Traverse, 1979

Type species. *Dyadospora murusattenuata* Strother and Traverse, 1979

(Due to the presence of naked, laevigate and permanently fused pseudodyads in the early Silurian (*Pseudodyadospora* Johnson, 1985), as well as similar enveloped forms (*Segestrespora* gen. nov.) the genus *Dyadospora* Strother and Traverse, 1979 is taken to include only non-enveloped laevigate dyads which habitually separate to produce two laevigate alete spores (see Burgess and Richardson 1991).

Dyadospora cf. *murusattenuata* Strother and Traverse, 1979

Plate 2, fig. 10

Figured specimen. FM 211, Pl. 2, fig. 10, slide Llan 8B/22, 138 1350, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Dimensions. Dyad 22 (28) 39 μm long, 20 (27) 37 μm wide at equator (5 specimens measured).

Biostratigraphic range. Early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. The few specimens recovered generally conform to the description of Strother and Traverse (1979), but preservation is too poor to be sure they are conspecific.

3. *Cryptospore monads*

This group encompasses monads whose wall thickness and sculpturing is comparable to that of the cryptospore tetrads and dyads but where it is more difficult to be convinced they are derived from land plants.

Genus RUGOSPHERA Strother and Traverse, 1979

Type species. *Rugosphaera tuscarorensis* Strother and Traverse, 1979

Rugosphaera cf. *R.?* *cerebra* Miller and Eames, 1982

Plate 2, figs 11 and 12

Figured specimens. FM 212, Pl. 2, fig. 11, slide Llan 8B/8, 110 1300; FM 213, Pl. 2, fig. 12, slide Llan 8B/24, 101 1080, both sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Description. Cryptospore monads sub-circular to circular in outline. In some specimens a laevigate inner body with a c. 1 μm thick wall can be discerned. Envelope always tightly adpressed to inner body and ornamented with closely spaced regularly sinuous to angular and rarely anastomosing rugulae 1(2)3.5 μm wide, 0.5–1 μm high and 0.5(1)1.5 μm apart.

Dimensions. Maximum diameter 23 (28) 37 μm , minimum diameter 16 (24) 30 μm (8 specimens measured).

Biostratigraphic range. Early Rhuddanian (*Acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Rugosphaera?* *cerebra* Miller and Eames is larger (38(45)55 μm in diameter), but otherwise similar. *R. tuscarorensis* Strother and Traverse has broader (1–4 μm) more widely spaced and less sinuous muri.

Genus STROPHOMORPHA Miller and Eames, 1982

Type species. *Strophomorpha ovata* Miller and Eames, 1982.

Strophomorpha ovata Miller and Eames, 1982

Plate 2, fig. 13

Figured specimen. FM 214, Pl. 2, fig. 13, slide Llan 3B/3, 035 1090, sample L8, Forestry Track F.33, Crychan Formation, *cyphus* Graptolite Biozone.

Description. Cryptospore monad with an elliptical to sub-rectangular outline and rounded poles. Body ornamented with low and rounded muri 0.75 (2) 3.5 μm wide separated by striae 1(2)3.5 μm across; muri are spirally arranged and converge at the poles. Wall is 1–3 μm thick and a single layer.

Dimensions. Maximum diameter 29 (46) 60 μm , minimum diameter 21 (29) 36 μm (10 specimens measured).

Biostratigraphic range. Late Rhuddanian (*cyphus* Graptolite Biozone; Text-fig. 7).

Comparisons. *Strophomorpha ovata* Miller and Eames is larger (48(56)65 μm) but in other ways closely comparable. *Moyeria cabottii* Cramer, 1966 is thinner-walled with narrower muri. *Qualisaspora fragilis* Richardson *et al.*, 1984 has two, much thinner, wall-layers.

Remarks. The presence of *Strophomorpha ovata* in the deeper-marine Rhuddanian aged sediments of the type Llandovery area, rather than the near-shore strata, indicates this species may be a thick-walled acritarch as opposed to a cryptospore. However, for the present it is described as a cryptospore until more evidence accumulates on its facies distribution.

Anteturma SPORITES H. Potonié, 1893

Turma TRILETES Reinsch, 1891

Subturma ZONOTRILETES Waltz, 1935 in Lubert and Waltz (1938)

Infraturma CRASSITI Bharadwaj and Venkatachala, 1961

Genus AMBITISPORITES Hoffmeister, 1959

Type specimens. *Ambitisporites avitus* Hoffmeister, 1959

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

Plate 2, fig. 15

Figured specimen. FM 95, Pl. 2, fig. 15, slide Llan 6/2, 071 1160, sample L21, Aeronian/Telychian type boundary section, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Dimensions. Diameter 20 (25) 30 μm (7 specimens measured).

Biostratigraphic range. Late Aeronian (*sedgwickii* Graptolite Biozone) to early Telychian (*turriculatus* Graptolite Biozone; Text-fig. 7).

Comparisons. *Ambitisporites?* *vavrdovii* Richardson, 1988 has triradiate splits, not sutures, in the proximal wall and a more prominent equatorial crassitude.

Ambitisporites? *vavrdovii* Richardson, 1988

Plate 2, figs 16–18

Figured specimens. FM 216, Pl. 2, fig. 16, slide Llan 7B/6, 090 1180, sample L1, Forestry Track F.33, Scrach Formation, *persculptus* Graptolite Biozone. FM 217, Pl. 2, fig. 17, slide Llan 8B/6, 138 1225, sample L5, Forestry Track F.33, Bronydd Formation, *acinaes* Graptolite Biozone; FM 218, Pl. 2, fig. 18, slide Llan 3B/1, 130 1296, sample L8, Crychan Formation, *cyphus* Graptolite Biozone.

Description. Amb sub-triangular to triangular. Equatorial crassitude 1–3 μm wide and well defined. Proximal surface laevigate. Trilete mark distinct, is a simple split without laesurae which extends to the equator or nearly so. Distal exine 1–2 μm thick and laevigate.

Dimensions. Diameter 28 (24) 32 μm (8 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Aeronian (*convolutus* Graptolite Biozone; Text-fig. 7).

Comparisons. Comparable 'trilete' spores have been described by Gray and Boucot (1971, lower Llandovery of North America), Gray *et al.* (1982, ?Caradoc of Libya), Johnson (1985, lower Llandovery of North America), and Richardson (1988, late Ordovician and early Llandovery of Libya). Moreover, Gray *et al.* (1982) have shown that closely comparable spores can be derived from mechanically fragmented tetrads of the genus *Tetrahedraletes*. *Ambitisporites avitus* Hoffmeister has its earliest records in the later Llandovery of North Africa and has more prominent trilete marks with sutures and laesurae, never a simple split.

COMPARISON WITH SIMILARLY AGED MICROFLORAS WORLDWIDE

Several continents have been recognized in the Silurian (Livermore *et al.*, 1985). These include Laurentia (North America and Europe north of the Iapetus suture), Baltica (Europe and Russia south of the Iapetus suture and north of the Hercynian suture), and Gondwana (Africa, South America and Australasia). Uppermost Ordovician and Llandovery spore microfloras from the type Llandovery area are compared with those from these continents.

Late Ordovician and early Silurian assemblages

Baltica. Vavrdova (1982, 1984, 1988) has described a diverse assemblage of cryptospore tetrads from the late Ordovician (*bohemicus* graptolite Biozone) Kosov Formation in Czechoslovakia. Many specimens appear similar, both in size, and sculptural patterning on their envelopes, to those from the type Llandovery area. For example, tetrad types A, B and C of Vavrdova (1984) are

similar to *Tetrahedraletes medinensis* var. *parvus*, *Velatitetras reticulata* and *Velatitetras* sp.A respectively. 'Trilete spores' (*Ambitisporites?* *vavrdovii*) were also recorded in Czechoslovakia.

Laurentia. Sporomorph assemblages from the late Ordovician and early Llandovery of North America are also similar to those from the type Llandovery area in that they are predominantly composed of cryptospores (Gray and Boucot 1971; Cramer and Diez 1972; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Gray 1988). In many of these studies (Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985) the North American cryptospore tetrads are considerably larger ($\bar{x} = c. 50 \mu\text{m}$) than those from the type Llandovery area ($\bar{x} = 26 \mu\text{m}$). However, those cryptospore tetrads obtained from upper Ordovician and basal Llandovery strata by Gray (1985, 1988) are of similar size ($\bar{x} = < 30 \mu\text{m}$) and some possessed highly comparable envelopes.

Ambitisporites? *vavrdovii* has also been recorded from the Llandovery of North America (Gray and Boucot 1971; Gray 1985).

Gondwana. A diverse assemblage of cryptospores has been recently described from subsurface material of late Ordovician to late Llandovery age in north-east Libya (Richardson 1988). This assemblage comprises around ten species of cryptospore tetrad, eleven species of pseudodyad, two species of true dyad, three species of cryptospore monad and three species of trilete miospore. Some of these are identical to those from the type Llandovery area, although eleven of the species discovered in Libya have not been seen in Britain.

Other late Ordovician and early Llandovery records of sporomorphs (all *Tetrahedraletes*) from Gondwana are from the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, South Africa (Gray *et al.* 1986); and from the Vila Maria Formation of the Parana Basin, Brasil (Gray *et al.* 1985). Furthermore, specimens of *Tetrahedraletes* recovered by Gray *et al.* (1982) from the ?Caradoc strata of the Murzurk Basin in Libya are closely comparable to uppermost Ordovician and lower Llandovery specimens from the type Llandovery area.

Late Llandovery assemblages

Late Llandovery sporomorph assemblages are known from Baltica, Laurentia and Gondwana (Hoffmeister 1959; Cramer 1968, 1969; Smith 1975; Emo and Smith 1978; Aldridge *et al.* 1979; Pratt *et al.* 1978; Smith 1979, 1981; Gray 1985; Hill *et al.* 1985; Gray 1988; Richardson 1988). All these investigations have demonstrated low spore diversity during this period with smooth-walled trilete miospores of the genus *Ambitisporites* predominating. This is comparable with the late Llandovery spore assemblage obtained from the type Llandovery area.

PALYNOFACIES

Preliminary investigation of the palynofacies in the type Llandovery area (Burgess 1987), has demonstrated large numbers of cryptospores and reworked acritarchs (Tremadoc and Ordovician) in the Scrach Formation and lower Bronydd Formation. This indicates deposition in nearshore palaeoenvironments, as previously suggested following mega fossil and sedimentological investigations (Cocks *et al.* 1984). Higher in the Bronydd Formation and throughout the Crychan, Trefawr, Rhydings, Wormwood, and Cerig Formations an extremely sparse microflora with few spores was obtained. The palynological assemblage, macro-fauna and sedimentology (Cocks *et al.* 1984) of these formations indicate deposition in off-shore shelf conditions at a considerable distance from land. It is thus probable that the sporomorph assemblage obtained from the base of the Llandovery type section is more representative of its age than that from the late Rhuddanian through to the early Telychian (later Telychian not sampled).

BIOSTRATIGRAPHY

Text-figure 7 presents the stratigraphical ranges of the sporomorphs recovered from the type Llandovery area. The two fold sub-division of the sequence is closely comparable to that recognized by Gray (1985, 1988), Richardson and McGregor (1986) and Richardson (1988).

Gray (1985) first noted the presence of a cryptospore-dominated spore assemblage in the Late Ordovician and Early Silurian and named this 'Microfossil Assemblage Zone 1'. It has recently been formally named the *Nodospora* sp. A (= *Velatitetras laevigata*) – *Dyadospora nurusdensa* Assemblage Biozone (Richardson 1988), and has been further subdivided into three Assemblage Biosubzones. Samples L1–L20, from the late *persculptus* to late *sedgwickii* Graptolite Biozones of the type Llandovery area, fall within the *Dyadospora membranifera* (= *Segestrespora membranifera*) – *Pseudodyadospora* sp. B Biosubzone of Richardson (1988). *Ambitisporites?* *vavrdovii* is present in this Biosubzone, but as these spores probably derive from mechanically fragmented cryptospore tetrads (Gray *et al.* 1982) they do not represent the earliest records of trilete miospores.

Gray (1985) also recognized a later Llandovery spore zone typified by smooth-walled trilete miospores and named it 'Microfossil Assemblage Zone 2'. This had been named the *Ambitisporites avitus* assemblage by Richardson (1974) and was later termed the *Ambitisporites dilutus* – *A. avitus* Assemblage Zone by Richardson and McGregor (1986). In the type Llandovery area this zone is recorded from samples L21–L23 (late Aeronian *sedgwickii* Graptolite Biozone to early Telychian *turriculatus* Graptolite Biozone).

The oldest specimens of *Ambitisporites dilutus* recorded from the late Aeronian (*sedgwickii* Graptolite Biozone) Wormwood Formation are the oldest known with precise dating. Their recovery enables the reference section for the base of the *Ambitisporites avitus* – *A. dilutus* spore Assemblage Zone of Richardson and McGregor (1986) to be defined as sample L21 (= locality 162 of Cocks *et al.* 1984) in the Type Aeronian/Telychian Boundary Section of the type Llandovery area.

A review of the literature suggests that the appearance of true *Ambitisporites* (not *Ambitisporites?* *vavrdovii*) occurs at comparable horizons globally. For instance, elsewhere in the British Isles *Ambitisporites* first occurs in the Aeronian *Pentamerus* Beds of the Welsh Borderland (Aldridge *et al.* 1979), and the Telychian *griestonensis* Graptolite Biozone of Ireland (Emo and Smith 1978; Smith 1981). Furthermore, in North America the incoming of *Ambitisporites* is placed at around the C2–C3 boundary (Gray 1985; 1988) which is equivalent to slightly lower in the Aeronian *sedgwickii* Graptolite Biozone than recorded in the type area. In North Africa *Ambitisporites* is also first recorded in the Aeronian (Hoffmeister 1959; Hill *et al.* 1985; Richardson and McGregor 1986; Richardson 1988).

PALAEOBOTANICAL IMPORTANCE

That cryptospores may provide evidence of pioneering land plants has been much debated (Gray and Boucot 1971, 1977; Gray 1985, 1988; Taylor, 1982). However, as they have yet to be recovered from the sporangia of a land-plant megafossil their derivation from this source remains unproven. The best evidence for a land plant source comes from their abundant recovery in fluvial sediments of North America (Johnson 1985; Strother and Traverse 1979), and their similarity to spores produced by certain extant hepatics (Gray 1985).

Trilete miospores, on the other hand, have been recovered from within the sporangia of the rhyniophytoid land plant *Cooksonia pertonii* in the late Silurian (Lang 1937; Fanning *et al.* 1988). Consequently, the Llandovery examples may be derived from a similar source and those from the late Aeronian may provide the oldest evidence of such organisms.

In this study the oldest cuticles probably derived from land plants (Edwards 1986) were recovered from the late Aeronian (Pl. 2, fig. 14). They are apparently absent in the Rhuddanian, even though these samples were the most nearshore investigated and sporomorphs were at their most abundant and diverse. Other studies have reported cuticles in the middle Caradoc and later Ordovician (Gray

et al. 1982; Gray 1985; Vavrdova 1988). Internally thickened tubes (Burgess and Edwards in press) were also not recorded from the type Llandovery area, even though Pratt *et al.* (1978) and Gray (1985) found them in upper Llandovery sediments of the USA, and they are present in basal Wenlock strata of the type Wenlock area (Burgess and Richardson 1991). Their absence may be related to the fact that extremely distal sediments were sampled in the late Llandovery of the type area. However, the facies in the early Rhuddanian are regarded as suitable for their recovery and their absence at this level may be genuine.

In conclusion, this study provides some evidence to support the assertions of Gray (1985) and Edwards and Burgess (1990), that a major change in the land-flora occurred in the late Aeronian. This change was from a flora dominated by cryptospore-producing plants, to a flora dominated by trilete miospore-producing plants. Moreover, this change appears to have occurred at approximately the same stratigraphical horizon worldwide.

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SILURIAN CRYPTOSPORES AND MIOSPORES FROM THE TYPE WENLOCK AREA, SHROPSHIRE, ENGLAND

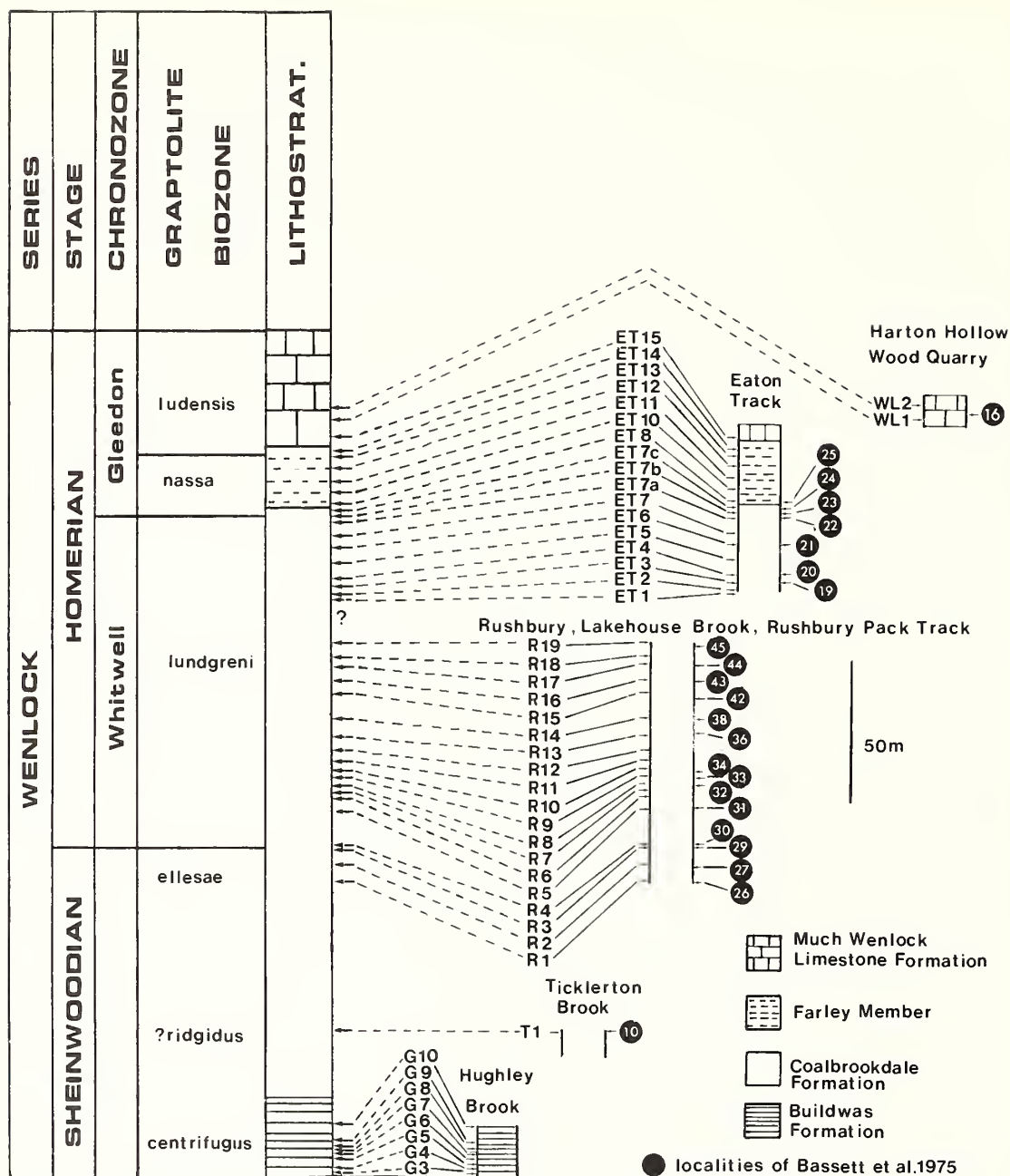
by N. D. BURGESS and J. B. RICHARDSON

ABSTRACT. The earliest occurrence of sculptured hilate cryptospores and miospores is near the base of the cf. *protophanus-verrucatus* Sporomorph Zone, now more accurately located within the *lundgreni* Graptolite Biozone in the type Wenlock area. Palynofacies studies indicate that this event is unrelated to changes in the depositional environment. All the Sheinwoodian sporomorphs are laevigate (six species) and have either a crassitate or patinate structure. The oldest known sculptured specimens of trilete miospores (two or three species) and hilate, crassitate/patinate cryptospores (four species) appear almost synchronously in the Homerian (upper part of *lundgreni* Graptolite Biozone). Additional sculptured taxa (two species) appear in the later Homerian but there are no innovations in structure. In North Africa (Gondwana) a closely comparable sequence of structural and sculptural events occurs. Three groups of sporomorphs described from the Buildwas, Coalbrookdale and lower Much Wenlock Limestone Formations are permanently fused cryptospore tetrads (one species), hilate cryptospores derived from dyads (eight species), and trilete miospore (six species). Systematic descriptions of seventeen species in eight genera are provided. Two genera *Laevolancis* and *Artemopyra*, three species *Laevolancis plicata*, *Hispanaediscus wenlockensis*, and *Artemopyra brevicosta*, and one combination are new, and the genera *Hispanaediscus* and *Dyadospora* are emended.

WENLOCK sporomorphs although known from only a few studies provide evidence for the existence of early land plants (Gray 1985) and hold a largely untapped potential for stratigraphical correlation (Richardson and McGregor 1986). Many of these assemblages contain mainly laevigate trilete miospores showing little diversity and have been obtained from poorly dated strata (Smith 1975; Colthurst and Smith 1977; Strother and Traverse 1979). Libyan assemblages are often superbly preserved (Richardson and Ioannides 1973) but although the sequence of spore sculptural patterns is closely similar to that in the Welsh Borderland, and the succession is dated by graptolites, there are samples which may be either Lower Ludlow or Upper Wenlock based on the latter. In some of these cases sporomorph data from the present study support a Wenlock age.

In contrast to North Africa, the geology of the type Wenlock area is well known (Bassett *et al.* 1975) and samples from higher parts of the sequence have yielded sporomorph assemblages of increasing diversity, although frequently spores are comparatively rare (1–20% of assemblage). Spores have been described from the type Wenlock area by Downie (1963), Richardson and Lister (1969), and Mabillard and Aldridge (1985) and from Dudley by Dorning (1983). Most previous works consist solely of records of the miospore genus *Ambitisporites*, but Richardson and Lister (1969) described eight miospore taxa, including some questionable miospores now regarded as cryptospores, and sculptured tetrads in the Much Wenlock Limestone Formation (Wenlock Limestone).

Sections in the type Wenlock area have been resampled (Text-fig. 1) to determine the diversity and stratigraphical ranges of the sporomorph taxa and, as precisely as possible, the horizons where sporomorph events occur, in particular the first appearance of sculpture in 'naked' cryptospores (i.e. those without envelopes) and in miospores. The advent of sculptural types is considered to have biological as well as biostratigraphical significance (Richardson and Lister 1969; Gray 1985;



TEXT-FIG. 1. Lithostratigraphic and biostratigraphic position of samples collected from the type Wenlock area, in relation to localities of Bassett *et al.* (1975).

Richardson 1985; Fanning *et al.* 1988). Such studies assist in attempts to understand the colonization of the land by plants because rocks of this age may contain abundant plant microfossils but few megafossils (Richardson and Ioannides 1973; Edwards and Fanning 1985; Gray 1985).

SAMPLING AND TECHNIQUES

Reconnaissance sampling at Eaton Track and Harton Hollow Wood Quarry by Richardson and Lister (1969), and later by the authors with the Ludlow Research Group, revealed laevigate and sculptured sporomorphs at Graptolite locality 24 of Bassett *et al.* (1975), near the top of the Eaton Track Section. For this study a total of forty eight samples were collected from six sections covering a stratigraphical interval of *c.* 240 m (Table 1) from basal Sheinwoodian (basal *centrifugus* Graptolite Biozone) to the late Homerian (lower part of the *ludensis* Graptolite Biozone) but excluding the upper *c.* 20 m of the Much Wenlock Limestone Formation. However, the uppermost part of the section has been sampled independently by both authors in the type Ludlow Area and so far has not yielded any new taxa. Details on the stratigraphy of the type Wenlock Area sections (except for Hughley Brook) are in Bassett *et al.* (1975).

TABLE 1. Locality and horizon of the sections studied

Section	Grid reference	Formation
Hughley Brook <i>c.</i> 400 m SW of Gippols Farm	SO 58009920	Buildwas
Ticklerton Brook	SO 48589042	Coalbrookdale
Rushbury	SO 51329173– SO 51329168	Coalbrookdale
Lakehouse Brook	SO 51399164	Coalbrookdale
Rushbury Pack Track	SO 51369146– SO 51679123	Coalbrookdale
Eaton Track	SO 50049001– SO 50509010	Coalbrookdale (Farley Member) – Much Wenlock Limestone
Harton Hollow Wood Quarry	SO 48148788	Much Wenlock Limestone

Samples were all fine-grained buff to olive-green calcareous siltstones and silty limestones. Palynomorphs were extracted and prepared for light microscope observation using standard techniques: HCl–HF–HCl acid treatment followed by zinc bromide solution (S.G. 2.0) heavy mineral separation. Organic residues were washed with distilled water between HCl and HF treatment to remove residual calcium ions and to reduce the formation of calcium fluoride and related compounds during HF treatment. Residues were sieved through a 10 μ m sieve, dried on coverslips, mounted in 'Elvacite' mounting medium, and studied in normal transmitted light and Nomarski Interference using a Zeiss Photomicroscope. Photomicrographs were taken on Ilford FP4 film.

From each sample 30 g of rock was processed and a measured amount of the residue from a known mass of rock mounted on a slide. Palynomorphs were then counted from a proportion of the slide and from this the absolute percentage per gram of sample was calculated for prasinophycean 'phycomata' (Tappan 1980) and each acritarch, cryptospore and miospore group. Palynomorph counts were made under oil at $\times 1000$.

SYSTEMATIC PALAEOONTOLOGY

The last decade has seen a number of reports showing that Upper Ordovician and Silurian strata contain spore-like microfossils in association with trilete miospores (Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Hill *et al.* 1985; Richardson 1988). We group these atypical spores (cryptospores *sensu* Richardson *et al.* 1984; Richardson 1988) into two major categories which are morphologically distinct and which may reflect macroplant groups and their evolution. In the descriptions below the terminology of Grebe (1971) is used to describe all sporomorphs, included cryptospores, but we have used the term *muri* for sinuous, sometimes anastomosing, ridges, whether or not they form a reticulum. The stratigraphical distribution refers to the range within this study.

Spore dimensions are given as the maximum diameter in polar compression unless stated otherwise, with the

minimum and maximum of the range presented and the mean in brackets. Figured specimens are stored in the Palynology Section, Palaeontology Department, British Museum (Natural History), London and have the prefix FM. Specimen co-ordinates are from a Zeiss Photomicroscope III no. 2562 housed in the Department. All specimens are also located by means of standard England Finder co-ordinates, and are ringed using a permanent red pen.

Anteturma CRYPTOSPORITES Richardson *et al.*, 1984

1. 'Permanently' fused cryptospore tetrads

This group comprises tetrads and dyads which are not found separated into their individual components and which we therefore believe are 'permanently' fused. Such forms are abundant in the lower Llandovery where well-preserved specimens are enclosed within variously sculptured envelopes (Strother and Traverse 1979; Miller and Eames 1982; Gray 1985, 1988; Johnson 1985; Burgess 1987). Occasionally individual specimens occur with poorly preserved proximal faces which may represent fragmented tetrads (Richardson 1988).

Genus TETRAHEDRALETES Strother and Traverse, 1979

Type species. Tetrahedraletes medinensis Strother and Traverse, 1979.

Tetrahedraletes medinensis Strother and Traverse, 1979

Plate 1, figs 12 and 13

Figured specimens. FM 156, Pl. 1, fig. 12, slide S24/3, 040 1210; FM 157, Pl. 1, fig. 13, slide S24/6 060 1240; both specimens from sample G 5, Hughley Brook, lower Buildwas Formation.

EXPLANATION OF PLATE 1

All figures $\times 1000$.

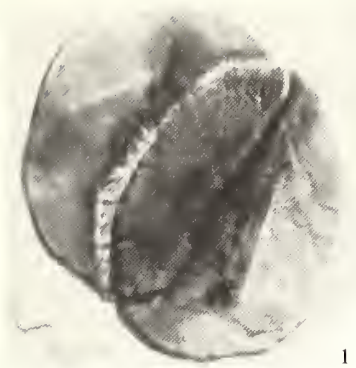
Figs 1–3. *Artemopyra brevicosta* sp. nov. 1, Dyad; FM 147 (slide GL22/1 co-ord 060 1030; England Finder no: F32/3/4), sample ET 7a, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 2, FM 148 (slide GL24/26 co-ord 200 1110; E.F. no: U40/4 U41/3), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 3, FM 146, holotype (slide ET 9A/4 co-ord 165 1300; E.F. no: R60), sample ET 10, Farley Member, *nassa* Graptolite Biozone.

Figs 4–9. *Hispanaedis discus wenlockensis* sp. nov. 4, FM 150 (slide GL24/23 co-ord 030 1263; E.F. no: C56/2), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 5, Proximal view showing radial muri; FM 151 (slide GL24/5 co-ord 130 1055; E.F. no: N35/3), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 6, Distal view showing verrucae; FM 149 (slide GL24/13 co-ord 100 1290; E.F. no: K59/4), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 7, Dyad; FM 153 (slide ET 9A/1 co-ord 090 1365; E.F. no: J67/2), sample ET 10, Farley Member, *nassa* Graptolite Biozone. 8, FM 152, holotype; proximal view (slide GL 24/24 co-ord 055 1205; E.F. no: E50/4 F50/2), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 9, Holotype, FM 152; distal view.

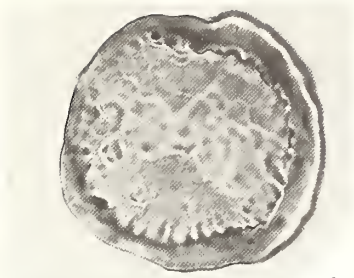
Figs 10 and 11. *Artemopyra* sp. A. 10, Proximal surface with radial muri and murus marking boundary of proximal hilum; FM 154 (slide ET 16/5 co-ord 078 1088; E.F. no: H38/2), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone. 11, Specimen showing muri on proximal surface and smooth distal surface; FM 155 (slide ET 16/8 co-ord 144 1050; E.F. no: 034/4 035/3), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

Figs 12 and 13. *Tetrahedraletes medinensis* Strother and Traverse 1979. 12, FM 156 (slide S24/3 co-ord 040 1210; E.F. no: E53), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone. 13, FM 157 (slide S24/6 co-ord 060 1240; E.F. no: G54/1/3), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone.

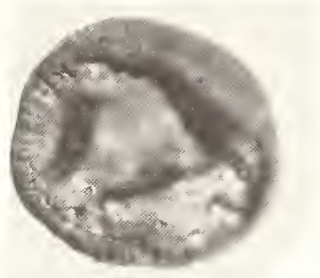
Figs 14 and 15. HILATE CRYPTOSPORE TYPE 1. 14, Sculptured distal surface; FM 158 (slide GL24/7 co-ord 100 1070; E.F. no: K36/4), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 15, Smooth 'proximal' surface of FM 158.



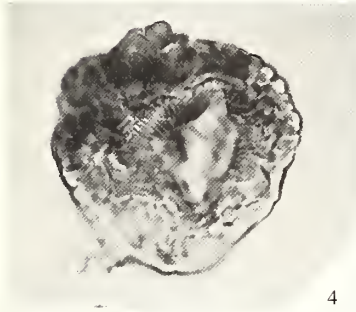
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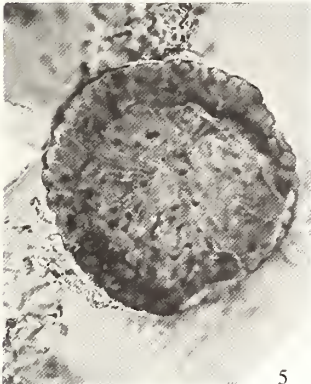
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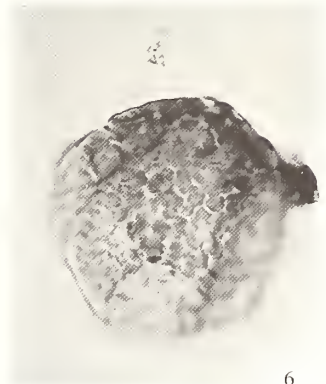
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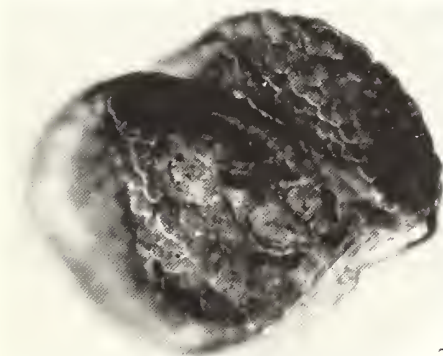
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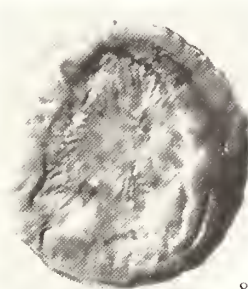
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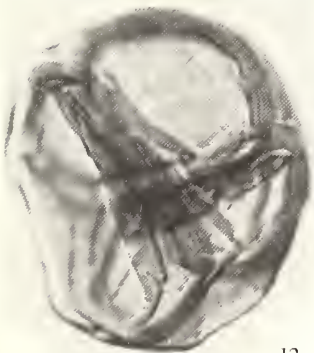
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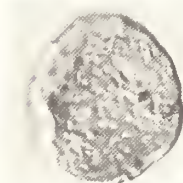
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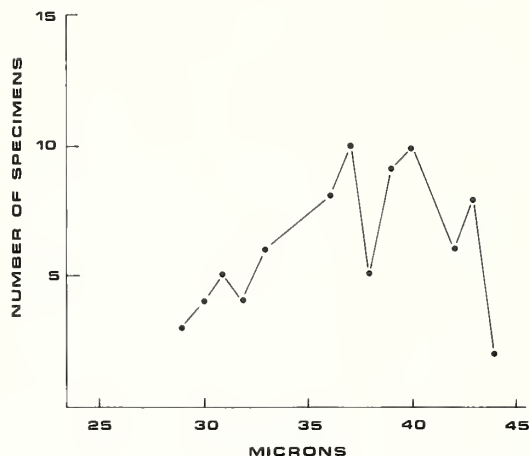
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Description. Laevigate obligate tetrahedral tetrads, subcircular to circular in outline, preserved in many compressional forms relating to the degree of rotation from an apical view prior to compression. Within the tetrads individual 'spores' have a subtriangular to subcircular equatorial outline, and unfused equatorial crassitudes 1–5 μm wide. Distal exine 1–2 μm thick and usually invaginated.

Dimensions. Tetrads 30(37)52 μm in diameter (100 specimens measured from sample G 5; Text-fig. 2).



TEXT-FIG. 2. Size frequency distribution of a hundred *Tetrahedraletes medinensis* (Strother and Traverse, 1979) from sample G 5, Hughley Brook (*centrifugus* Graptolite Biozone); $\bar{x} = 37.3 \mu\text{m}$.

Distribution. Throughout the Wenlock, basal Sheinwoodian to late Homerian Stages, *centrifugus* to *ludensis* Graptolite Biozones.

Comparisons. Specimens of *Tetrahedraletes medinensis* recovered in the Wenlock (Text-fig. 2) are larger than those from the Rhuddanian of the type Llandovery area (Burgess 1991) but are similar in size to those from the Llandovery of North America (Pratt *et al.* 1978; Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985).

2. Hilate cryptospores

Sporomorphs in this group are alete, hemispherical in equatorial view, have a thin proximal surface (hilum) and an equatorial thickening. In many cases they are seen to be derived from loosely attached dyads and as all have the same basic structure they are probably all derived from dyads.

Genus LAEVOLANCIS gen. nov.

Type species. *Laevolancis (Archaeozonotrilletes) divellomedium* (Chibrickova) comb. nov.

Diagnosis. Alete proximally hilate cryptospores, originally elliptical to hemispherical in equatorial view with an equatorial to subequatorial crassitude surrounding the hilum; exine laevigate.

Derivation of name. Latin *laevigatus*, smooth; *lancis*, plate or dish.

Remarks. These cryptospores are occasionally seen as loosely attached dyads.

Discussion. The genus *Gneudhaspora* Balme (1988) includes similar spores but is not used here because the Australian spores may be trilete, monolete or alete. The Wenlock spores are all alete and many, if not all, are derived from dyads. Consequently we have erected a new genus *Laevolancis*

to accommodate the alele forms in Balme's genus and other alele species of similar structure with a laevigate exine.

Laevolancis divellomedium (Chibrickova) comb. nov.

Plate 2, figs 4 and 6.

- 1959 *Archaeozonotriletes divellomedium* Chibrickova, p. 65, pl. 9, fig. 4.
- 1966 *Hispanaedis discus berneseae* Cramer, p. 82, pl. 1, fig. 1; text-fig. 2, figs 2 and 11.
- 1968 Spore no. 2651, Magloire, pl. 1, fig. 6.
- 1969 ?*Archaeozonotriletes* cf. *divellomedium* Chibrickova; Richardson and Lister, p. 238, pl. 43, fig. 12.
- 1973 ?*A.* cf. *divellomedium* Chibrickova; Richardson and Ioannides, p. 280, pl. 8, figs 10 and 11.
- 1974 *Zonales* (?) *divellomedium* (Chibrickova); Arkhangelskaya, pl. 6, figs 3 and 4.
- 1974 ?*A. divellomedium* Chibrickova; McGregor, pl. 1, figs 35 and 40.
- 1978 *Hispanaedis* sp., McGregor and Narbonne, p. 1296, pl. 1, figs 20–22.
- 1979 'Smooth-walled inaperturate spore', Strother and Traverse, p. 14, pl. 12, fig. 9.
- 1984 ?*Stenozonotriletes irregularis* McGregor, p. 37, pl. 1, fig. 26.
- 1986 *Tholisporites divellomedium* Turnau, p. 349, pl. 2, fig. 12.
- 1980 *Zonales* (?) *divellomedium* (Chibrickova) Arkhangelskaya, pl. 5, fig. 34.
- 1988 *Gneudnasporea divellomedium* (Chibrickova) Balme, p. 125 [partim], pl. 3, figs 1–7.

Holotype and type locality. Chibrickova, 1959, prep. 977, collections of the Gorno-Geological Institute, Bashkir Filial, Academy of Sciences, USSR; Takata Beds, Emsian.

Figured specimens. FM 163, Pl. 2, fig. 4, slide S24/3, 145 1290, sample G5, Hughley Brook, Buildwas Formation; FM 164, Pl. 2, fig. 6, slide ET 8/5, 133 1265, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Diagnosis. A *Laevolancis* with a rigid wall and a 1(1.5)4 μm wide subequatorial crassitude.

Description. Cryptospores occasionally preserved in loosely attached dyads in a variety of compressional morphologies but are usually separated. Separated spores: amb subcircular, or occasionally circular, specimens frequently tipped, originally roughly hemispherical in equatorial view with $\pm$ flattened proximal polar area. An equatorial to subequatorial crassitude surrounds the proximal hilum; hilum flattened to concave in equatorial view, laevigate, occasionally folded, or ruptured, optically appears thinner than the distal exine; distal exine laevigate c. 2 μm thick.

Dimensions. Maximum diameter 30(38)49 μm , minimum diameter 18(30)38 μm (30 specimens measured from sample G 5, Hughley Brook, Buildwas Formation).

Distribution. Present and often common throughout the sequence, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The size range of Chibrickova's specimens (35–50 μm ; Chibrickova 1959) overlaps with that of the Wenlock specimens. Balme's specimens from the Devonian Gneudna Formation (Balme 1988) also overlap but are mostly larger (44–68 μm); otherwise the alele forms described by Balme are identical (J.B.R., examination of the Australian material). *Hispanaedis discus berneseae* Cramer, 1966 is regarded as synonymous but the genus *Hispanaedis* is restricted herein to verrucate hilate cryptospores similar to the type species.

Laevolancis plicata sp. nov.

Plate 2, fig. 8

Holotype and type locality. FM 167; Pl. 2, fig. 8; slide Rush S14/5, 170 1150; sample R 17, Rushbury Pack Track (Text-fig. 1; Table 1), Coalbrookdale Formation, late Wenlock *lundgreni* Graptolite Biozone.

Diagnosis. A *Laevolancis* with thin, often folded, walls.

Derivation of name. Latin *plicatus*, folded.

Description. Cryptospores occasionally preserved in loosely attached, often partially separated, dyads but spores are most frequently found separated as single grains. Amb sub-circular to circular; distally slightly convex in equatorial view. Crassitude equatorial to sub-equatorial, 0.5–1.5 μm wide, surrounds a proximal hilum; proximal hilum usually concave, laevigate and frequently folded. Distal exine *c.* 1 μm thick, laevigate.

Dimensions. Maximum diameter 22(27)35 μm , minimum diameter 14(21)27 μm (30 specimens measured from sample ET 7c); Eaton Track Section, Coalbrookdale Formation.

Distribution. Present throughout the sequence, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. *Laevolancis divellomedium* (Chibrickova) comb. nov. is larger, more inflated distally and has a thicker, more rigid wall (*c.* 2 μm). Many of these spores are separated from dyads of the genus *Dyadospora* (Strother and Traverse, 1979) emend. and possibly solely from *D. murusattenuata*.

Genus HISPANAEDISCUS (Cramer) emend.

Type species. *Hispanaediscus verrucatus* Cramer, 1966.

Emended diagnosis. Alete proximally hilate cryptospores; originally elliptical to hemispherical in equatorial view; equatorial to sub-equatorial crassitude surrounding the hilum. Hilum laevigate, or

EXPLANATION OF PLATE 2

All figures $\times 1000$.

Figs 1–3, 5. *Dyadospora murusdensa* (Strother and Traverse) emend. 1, FM 159 (slide Tick S1/7 co-ord 063 1209; E.F. no: F51/1/3), sample T 1, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. 2, Partially separated specimen with pyrite damage, FM 161 (slide Rush S 10/8 co-ord 200 1204; E.F. no: U50/4), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 3, FM 160 (slide ET 5A/5 co-ord 152 1053; E.F. no: P35/3), sample ET 3, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 5, partially separated specimen; FM 162 (slide Rush S10/1, co-ord 070 1220; E.F. no: G52/2/G53/1), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

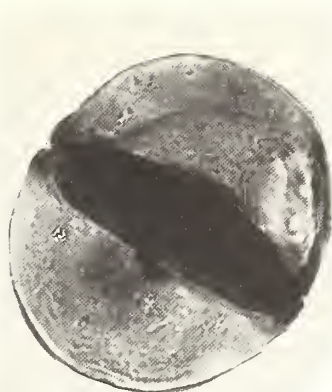
Figs 4 and 6. *Laevolancis divellomedium* (Chibrickova) comb. nov. 4, FM 164, holotype (slide ET 8/5 co-ord 133 1265; E.F. no: N56/4/N57/3), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 6, FM 163 (slide S24/3 co-ord 145 1290; E.F. no: P59/2/P60/1), sample G 5, Buildwas Formation, *centrifugus* Graptolite Biozone.

Figs 7 and 9. *Dyadospora murusattenuata* (Strother and Traverse) emend. 7, FM 165 (slide GL24/25 co-ord 098 1202; E.F. no: K50), sample ET 7c, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. 9, FM 166 (slide Rush S10/8 co-ord 153, 1204; E.F. no: P50), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

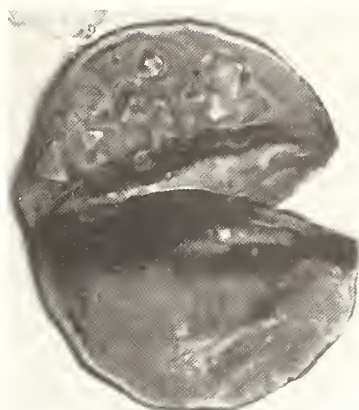
Fig. 8. *Laevolancis plicata* sp. nov. FM 167, holotype (Rush S14/5 co-ord 170 1150; E.F. no: Q44), sample R 17, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.

Figs 10 and 11. cf. *Hispanaediscus* sp. A. 10, FM 168 (slide ET 16/5 co-ord 090 1140; E.F. no: J44/1/2), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone. 11, FM 169 (slide ET 16/2 co-ord 160 1210; E.F. no: Q51/3), sample ET 15, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

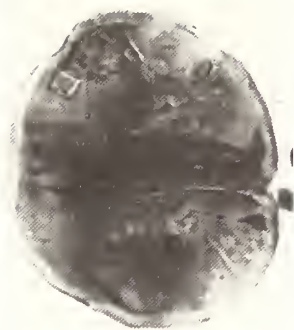
Figs 12 and 13. *Hispanaediscus verrucatus* (Cramer) emend. 12, FM 170 (slide Rush S14/5 co-ord 065 1040; E.F. no: F33), sample R 17, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. 13, FM 171 (slide ET 8/6 co-ord 017 1350; E.F. no: A65/2), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone.



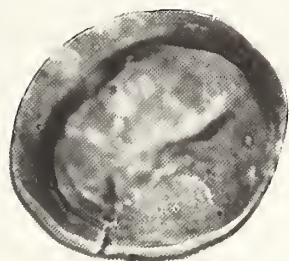
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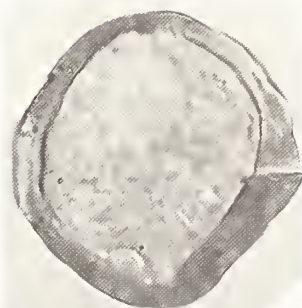
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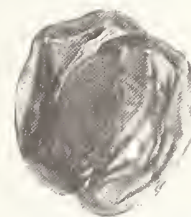
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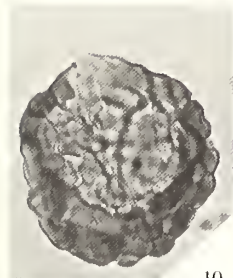
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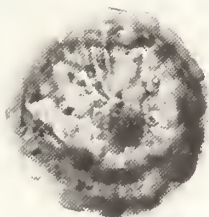
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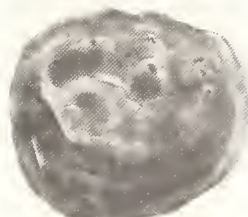
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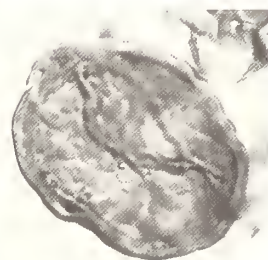
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with radial and/or randomly orientated muri/folds. Distal exine ornamented with verrucae and or muri.

Comparison. *Artemopyra* gen. nov. has the same structure and radial proximal muri/folds, but is distally laevigate, apiculate or spinose.

Remarks. Hilate cryptospores in *Hispanaedisus* are occasionally seen as loosely attached dyads. This genus was originally erected by Cramer (1966) for alele palynomorphs with laevigate, verrucate/murornate and foveolate sculpture. The type species is verrucate and we have restricted the genus to forms with verrucate distal sculpture where the proximal exine is not markedly thinner than the distal and included species with proximal sculpture.

Hispanaedisus verrucatus (Cramer) emend.

Plate 2, figs 12 and 13

- 1966 *Hispanaedisus verrucatus* Cramer, p. 82, pl. 2, fig. 7 [*partim*], non fig. 2.
 ?1969 cf. *Synorisporites verrucatus* Richardson and Lister, pl. 40, fig. 13.
 1973 cf. *Synorisporites verrucatus* Richardson and Lister; Richardson and Ioannides, p. 278, [*partim*] pl. 6, figs 17, 18, 20, non pl. 6, fig. 19.

Holotype. Cramer, 1966, pl. 2, fig. 7; F: 22354-5-2. San Pedro Formation, near Valporquero, León, northwest Spain. Probably of late Silurian age.

Figured specimens. FM 170, Pl. 2, fig. 12, slide Rush 13/14, 065 1040, sample R 16, Rushbury Pack Track, Coalbrookdale Formation; FM 171, Pl. 2, fig. 13, slide ET 8/6, 017 1350, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Emended diagnosis. An *Hispanaedisus* with a smooth, diaphanous hilum and verrucate – murornate distal sculpture.

Description. Hilate cryptospores probably derived from loosely attached, partially separated, dyads, but all specimens seen are single grains. Amb sub-circular to circular, originally distally hemispherical in equatorial view and flattened proximally. Distal exine more or less convex, c. 1 μ m thick, sculpture consists mainly of low verrucae and/or muri 1–5 μ m wide, c. 1 μ m high and 0.5–3 μ m apart. The groups of fused elements may coalesce into longer occasionally convolute and anastomosing muri.

Dimensions. Maximum diameter 23(28)32 μ m, minimum diameter 22(25)30 μ m (15 specimens measured).

Distribution. Upper Coalbrookdale Formation, Farley Member, and Much Wenlock Limestone Formation; upper *lundgreni* to lower *ludensis* Graptolite Biozones.

Comparisons. Some of Cramer's specimens appear identical to those from the Wenlock of the type area and Wenlock–Ludlow of North Africa. The spores from England, Spain and North Africa all have size ranges less than 35 μ m, and means of between 24 and 28 μ m. *H. wenlockensis* is larger and has proximal radial muri.

Remarks. Cramer's material appears to include trilete spores with a more triangular outline, similarly the material described by Richardson and Ioannides includes tetrads with comparable sculpture. Herein *H. verrucatus* is restricted to alele hilate cryptospores with a circular or subcircular amb.

Hispanaediscus wenlockensis sp. nov.

Plate 1, figs 4–9

Holotype and type locality. FM 152, Pl. 1, figs 8 and 9, slide GL 24/24, 055 1205, sample ET 7c, Eaton Track (Text-fig. 1 and Table 1), Coalbrookdale Formation, late Wenlock *nassa* Graptolite Biozone.

Paratypes. FM 149, Pl. 1, fig. 6, GL24/13, 100 1290, sample ET 7c; FM 150, Pl. 1, fig. 4, slide GL24/23, 030 1263, sample ET 7c; FM 151, Pl. 1, fig. 5, slide GL24/5, 130 1055, sample ET 7c; FM 152, Pl. 1, fig. 8, slide GL24/24, 055 1205, sample ET 7c, Coalbrookdale Formation; FM 153, Pl. 1, fig. 7, ET 9A/1, 090 1365, sample ET 8, Farley Member; all specimens from Eaton Track.

Diagnosis. An *Hispanaediscus* with short proximal radial muri and distal sculpture dominated by verrucae which occasionally coalesce into muri.

Description. Cryptospores derived from loosely attached, partially separated, dyads (only 1 found, Pl. 1, fig. 7) but most spores found separated as single grains. Amb sub-circular to circular; spores weakly convex distally in equatorial view. Crassitude equatorial to sub-equatorial, 0.5(1)1.5 μm wide, surrounds a proximal hilum. Proximal hilum sculptured by closely packed radial muri, up to 7 μm long and *c.* 1 μm wide which never reach the proximal pole. Distal exine *c.* 2 μm thick, sculptured with closely packed verrucae usually appearing hexagonal in plan view, elements 1(2)3 μm wide at the base, 1–1.5 μm high and 1 μm or less apart; rare elements composed of coalescent verrucae (muri) up to 17 μm long.

Dimensions. Maximum diameter 35(39)47 μm , minimum diameter 19(34)39 μm (27 specimens measured from sample ET 7c, Coalbrookdale Formation, Eaton Track).

Distribution. Uppermost Coalbrookdale Formation and lower Farley Member, lower *nassa* Graptolite Biozone.

Comparisons. *Hispanaediscus verrucatus* Cramer (1966) is smaller (*c.* 25 μm), laevigate proximally and has more widely spaced distal verrucae.

cf. *Hispanaediscus* sp. A

Plate 2, figs 10 and 11

Figured specimens. FM 168, Pl. 2, fig. 10, slide ET 16/5, 090 1140, sample ET 15, Eaton Track, Much Wenlock Limestone Formation; FM 169, Pl. 2, fig. 11, slide ET 16/2, 160 1210, sample ET 15, as above.

Description. Cryptospores seen only as separate grains. Amb circular, rarely subcircular; originally distally hemispherical and $\pm$ flattened proximally. Proximal hilum thin, usually absent or fragmentary; sculptured with low convolute to straight, radial muri or folds 0.5–1.5 μm wide and 7–10 μm long; muri/folds taper from margin of hilum to proximal pole. Distal exine *c.* 2 μm thick at the distal pole and slightly thickened, up to 3 μm thick at the equator; most specimens sculptured with closely spaced, convolute and anastomosing muri, rounded in profile, 0.5(2)4 μm wide, < 1–3 μm apart and < 1 μm high; elements usually composed of coalescent verrucae but may be more regular forming narrow irregular ridges or rugulae.

Dimensions. Maximum diameter 19(25)36 μm , minimum diameter 17(22.5)29 μm (13 specimens measured from samples ET 15, WL1 and WL2).

Distribution. Upper Coalbrookdale Formation, Farley Member and Much Wenlock Limestone Formation; lower *nassa* to lower *ludensis* Graptolite Biozones.

Comparison. Specimens of *Cymbosporites verrucosus* Richardson and Lister, 1969 are similar but larger (29–52 μm), some specimens have trilete folds or indistinct trilete marks, and the verrucae are larger and do not form ridges. cf. *Hispanaediscus* sp. A has a thin proximal hilum, and therefore is

not typical of the genus *Hispanaedisus*. Too few specimens have been found to warrant further taxonomic separation.

Genus ARTEMOPYRA gen. nov.

Type species. *Artemopyra brevicosta* sp. nov.

Derivation of name. Greek *artema*, ear-ring, pyr = fire.

Diagnosis. Alete proximally hilate cryptospores; originally elliptical to hemispherical in equatorial view. Proximal hilum sculptured with predominantly radial muri. Distal exine laevigate or sculptured with grana, coni, bifurcated elements or spines.

Remarks. Specimens have been found in loosely attached dyads.

Artemopyra brevicosta sp. nov.

Plate 1, figs 1–3

1973 ?*Emphanisporites* cf. *protophanus* Richardson and Ioannides, pl. 2, fig. 7.

1979 ? 'Spore with radial thickenings on one surface', Strother and Traverse, p. 14.

Holotype and type locality. FM 146, Pl. 1, fig. 3, slide ET 9A/4, 165 1300; sample ET 8, Eaton Track (see Text-fig. 1 and Table 1), Farley Member, late Wenlock *nassa* Graptolite Biozone.

Paratypes. FM 147, Pl. 1, fig. 1, slide GL 22/1, 060 1030, sample ET 7a; FM 148, Pl. 1, fig. 2, slide GL 24/26, 200 1110, sample ET 7c; both Eaton Track, upper Coalbrookdale Formation.

Derivation of name. Latin *brevis*, short; *costa*, rib.

Diagnosis. An *Artemopyra* with simple proximal subequatorial radial muri < half spore radius in length; distal exine laevigate.

Description. Proximally hilate cryptospores derived from loosely attached, partially separated, dyads; dyads frequent (Pl. 1, fig. 1), but most spores found separated as single grains. Amb circular to sub-circular, cryptospores originally hemispherical with flattened proximal pole. A more or less equatorial crassitude, distinct to indistinct, surrounds the hilum and is roughly circular and concentric with the amb; hilum sculptured with straight or slightly sinuous muri < 1(3)6 μm long, < 1(1)2 μm maximum width and < 1–2 μm apart; muri taper polewards. Distal exine laevigate, c. 1.5 μm thick.

Dimensions. Maximum diameter 22(35)49 μm , minimum diameter 21(28)44 μm (90 specimens measured from sample ET 7c).

Distribution. Upper Coalbrookdale Formation, Farley Member, upper *lundgreni* to lower *nassa* Graptolite Biozones.

Comparison. ?*Emphanisporites* cf. *protophanus* Richardson and Ioannides, 1973 from the Tannezuft and Acacus Formations of western Libya (probably upper Wenlock, Ludlow and Downton (Pridoli) equivalents) is slightly smaller but includes synonymous spores. Wenlock(?) material of Strother and Traverse (1979) has been examined and contains specimens of *A. brevicosta*, including dyads. *Artemopyra* sp. A has narrower, longer and more convolute radial muri.

Remarks. This species is distinctive and abundant and, in the type Wenlock Area, its first appearance is a good indicator of the late Homerian.

Artemopyra sp. A

Plate 1, figs 10 and 11

Figured specimen. FM 154, Pl. 1, fig. 10, slide ET 16/5, 078 1088; FM 155, Pl. 1, fig. 11, slide ET 16/8, 144 1050; both specimens from sample ET 15, Eaton Track, lower Much Wenlock Limestone Formation.

Description. Amb circular to sub-circular, cryptospores originally elliptical with flattened proximal pole. Crassitude equatorial to sub-equatorial, forms a narrow ring *c.* 1 μm wide surrounding the proximal hilum. Proximal hilum concave, sculptured with low, more or less radial muri and/or folds 2(4)7.5 μm long, *c.* 1 μm wide, < 1–1 μm apart and < 1 μm high; muri taper gradually to the proximal pole, becoming more convolute and anastomosing. Distal exine *c.* 1 μm thick and laevigate.

Dimensions. Maximum diameter 28 μm , minimum diameter 23 μm (two specimens measured from samples ET 15 and WL1).

Distribution. Found in two samples, Much Wenlock Limestone Formation, lower *ludensis* Graptolite Biozone.

Comparisons. *Artemopyra brevicosta* sp. nov. has shorter, more robust, radial muri.

HILATE CRYPTOSPORE type 1

Plate 1, figs 14 and 15

?1966 *Hispanaediscus leonensis* Cramer, p. 83, pl. 2, fig. 8

?1979 'Perforated palynomorph', Strother and Traverse, p. 14.

Figured specimen. FM 158, Pl. 1, figs 14 and 15, slide GL 24/7, 100 1070; sample ET 7c, Eaton Track, Coalbrookdale Formation.

Description. Proximally hilate cryptospores. Amb circular to sub-circular; cryptospores originally elliptical with flattened proximal pole. Crassitude equatorial to sub-equatorial, forms a narrow ring *c.* 1.5 μm wide surrounding the proximal hilum which is concave and laevigate. Distal exine *c.* 1.5 μm thick, foveolate; foveolae regularly spaced *c.* 1 $\mu\text{m} \times 0.5 \mu\text{m}$ and *c.* 1 μm apart.

Dimensions. Maximum diameter 18(21)25 μm (2 specimens recorded in sample ET 7c).

Distribution. As for figured specimen.

Comparison. *Hispanaediscus leonensis* Cramer, 1966 has a similar structure and may be synonymous with this type. However, the genus *Hispanaediscus* is used here for verrucate/murinate hilate cryptospores and hence could not be used for this type. Material from Pennsylvania described by Strother and Traverse (1979) has been re-examined by N.D.B. and contains specimens which are closely comparable.

3. *Dyads of hilate cryptospores*

In rocks of Llandovery age cryptospore tetrads and dyads are common and in most cases the tetrad or dyad condition is 'permanent'. For these propagules separate genera have been created. In younger Silurian strata intact dyads become increasingly rare although the hilate cryptospores derived from them are common. In this work the separated cryptospores are named whereas usually their dyad counterparts are not. This parallels the standard treatment of dispersed miospores and their tetrads. Because this is a gradational phenomenon the hilate cryptospore genus *Dyadospora* Strother and Traverse, 1979 is retained, though emended, pending further investigations.

Genus DYADOSPORA Strother and Traverse emend.

Type species. *Dyadospora nurusattenuata* Strother and Traverse, 1979 emend.

Emended diagnosis. Dyads composed of two laevigate hilate cryptospores. Individual spores not strongly mutually attached, a clear line of separation is always seen; in equatorial compression the two spores are often partially separated.

Remarks. The diagnosis of the genus *Dyadospora* has been restricted to include only non-‘permanent’ dyads which separate to give two laevigate hilate cryptospores. Pseudodyads, characteristic of the early Silurian, are retained in the genus *Pseudodyadospora* Johnson, 1985. With careful observation the two genera can be distinguished and their stratigraphical distribution and biological significance assessed.

Dyadospora murusattenuata Strother and Traverse emend.

Plate 2, figs 7 and 9

- 1979 *Dyadospora murusattenuata* Strother and Traverse, p. 15, pl. 6, figs 8 and 10.
 1982 *Dyadospora murusattenuata* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 8.
 1985 *Dyadospora murusattenuata* Strother and Traverse; Johnson, p. 334.

Figured specimens. FM 165, Pl. 2, fig. 7, slide GL24/25, 098 1202, sample ET 7c, Eaton Track; FM 166, Pl. 2, fig. 9, slide Rush S10/8, 153 1204, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation.

Emended diagnosis. A *Dyadospora* with thin folded walls.

Description. Dyads, usually isomorphic, circular to subcircular in equatorial view, usually preserved in oblique compression, each spore is distally convex; crassitudes at the point of contact between the two cryptospores; a cleft is always present between the crassitudes of each spore. Distal exine laevigate, c. 1 μ m thick over the distal pole and usually folded.

Dimensions. Dyad length 22(28)39 μ m, equatorial width 20(27)37 μ m (35 specimens measured) from sample ET 7c, Coalbrookdale Formation, upper Wenlock *nassa* Graptolite Biozone.

Distribution. Throughout the sequence, Buildwas to Much Wenlock Limestone Formations; lower *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The holotype of *Dyadospora murusattenuata* Strother and Traverse, 1979 (? Wenlock, pl. 3, fig. 9) is closely similar to the specimens found in this study. In both cases the specimens are thin-walled, folded and show partially separated dyads. Slides of the material from Pennsylvania described by Strother and Traverse have been examined for comparison and contain abundant dyads identical to those described herein. *D. murusdensa* Strother and Traverse, 1979 emend. is larger and thicker-walled. *Pseudodyadospora laevigata* Johnson, 1985 is more elongate, and often anisomorphic (i.e. the two parts of the dyad are of unequal size, Richardson 1988; Burgess 1991) and the individual ‘spores’ are joined by a single fused thickening, or crassitude.

Remarks. Separation of these dyads is believed to produce spores of the species *Laevolancis plicata* gen. et sp. nov.

Dyadospora murusdensa Strother and Traverse emend.

Plate 2, figs 1–3, 5

- 1979 *Dyadospora murusdensa* Strother and Traverse, p. 15, pl. 3, figs 6 and 7.
 1982 cf. *Dyadospora murusdensa* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 7.
 1985 cf. *Dyadospora murusdensa* Strother and Traverse; Johnson, p. 334, pl. 7, fig. 9.
 1985 *Dyadospora murusdensa* Strother and Traverse; Richardson in Hill *et al.*, p. 29, pl. 15, figs 8 and 9.

Figured specimens. FM 159, Pl. 2, fig. 1, slide Tick 1/7, 063 1209; sample T 1, Ticklerton Brook, Coalbrookdale Formation; FM 160, Pl. 2, fig. 2, slide ET 5A/5, 152 1053, sample ET 3, Eaton Track, upper Coalbrookdale Formation; FM 161, Pl. 2, fig. 3, slide Rush S10/8, 200 1204, sample R 14; FM 162, Pl. 2, fig. 5, slide Rush S10/1, 070 1220, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation.

Emended diagnosis. A *Dyadospora* with unfolded walls.

Description. Dyads, usually isomorphic, circular to subcircular in equatorial view, usually preserved in oblique compression, each spore is distally convex; crassitudes $2(3)4\ \mu\text{m}$ thick, equatorial to sub-equatorial, the two cryptospores are usually loosely attached or almost separated (Pl. 2, figs 2 and 5). In equatorial view the length is equal to, or slightly greater than the width at the equator; exine laevigate, $1(2)3\ \mu\text{m}$ thick over the distal pole and usually without folds.

Dimensions. Dyad length $23(39)47\ \mu\text{m}$, equatorial diameter $21(34)46\ \mu\text{m}$ (13 specimens measured from various samples).

Comparison. The holotype of *Dyadospora murusdensa* Strother and Traverse (1979, pl. 3, fig. 9) is closely similar to the dyads described above. Slides of material described by Strother and Traverse from Pennsylvania have been examined for comparison and contain dyads identical to those described here. *Dyadospora murusattenuata* Strother and Traverse emend. is thinner-walled and generally smaller.

Anteturma SPORITES H. Potonié, 1893

Turma TRILETES Reinsch, 1891

Subturma ZONOTRILETES Waltz, 1935 in Lubert and Waltz (1938)

Infraturma CRASSITI Bharadwaj and Venkatachala, 1961

Genus AMBITISPORITES Hoffmeister, 1959

Type species. *Ambitisporites avitus* Hoffmeister, 1959

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

Text-fig. 3D-H

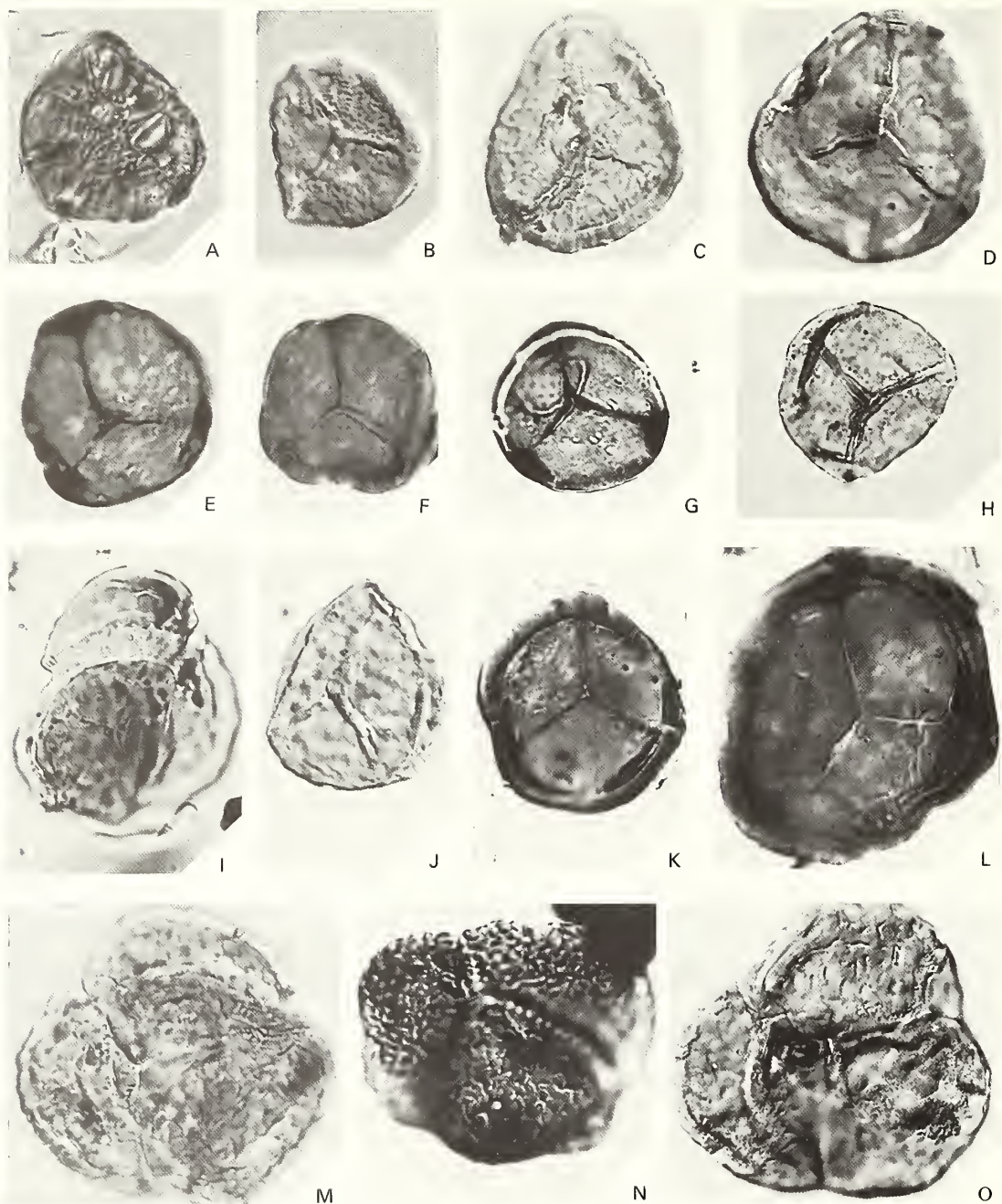
Figured specimens. FM 175, Text-fig. 3D, slide ET 16/2, 100 1205; sample ET 15, Eaton Track, Much Wenlock Limestone Formation; FM 176, Text-fig. 3E, slide Rush Vill S1/3, 182 1223, sample R 2, Rushbury, lower Coalbrookdale Formation; FM 177, Text-fig. 3E, slide ET 8/5, 130 1240, sample ET 6; FM 178, Text-fig. 3G, slide Rush Vill S1/3, 180 1050, sample R 2; FM 179, Text-fig. 3H, slide ET 8/5, 123 1380, sample ET 6, Rushbury and Eaton Track; specimens FM 177 and FM 179 are from the upper Coalbrookdale Formation and FM 178 from the lower Coalbrookdale Formation.

Dimensions. Diameter $22(28)47\ \mu\text{m}$ (100 specimens measured, see Text-fig. 4 for spread of measurements), distal exine $1-2\ \mu\text{m}$ thick.

Distribution. Common throughout the sequence. Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparison. *Ambitisporites avitus* Hoffmeister, 1959 has a well-defined crassitude.

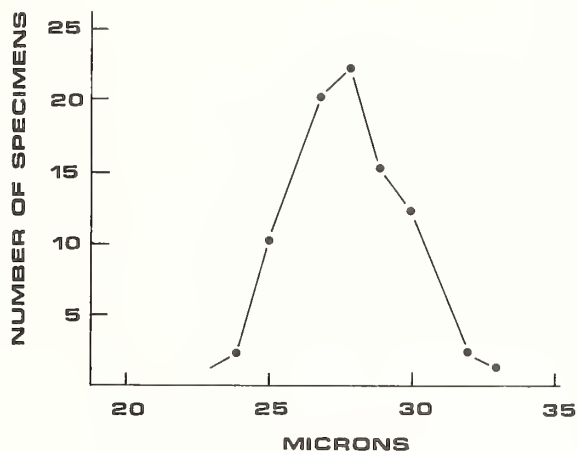
Remarks. *Ambitisporites dilutus* is the most abundant spore in the samples studied, up to 10,000 specimens per gram of sediment were present in some residues. The size-distribution of these spores



TEXT-FIG. 3. All figures $\times 1000$. A–C. TRILETE MIOSPORE TYPE 1. A, FM 172 (slide Rush S10/4 co-ord 135 1090; E.F. no: 039/1), sample R 14, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. B, FM 173 (slide GL22/1 co-ord 063 1048; E.F. no: F34), sample ET 7a, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. C, FM 174 (slide ET 9A/1 co-ord 070 1145; E.F. no: G44/4), sample ET 8, upper Coalbrookdale Formation, *nassa* Graptolite Biozone. D–H, *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. D, FM 175 (slide ET 16/2, co-ord 100 1205; E.F. no: K50/2), sample ET 15, lower Much Wenlock

shows a classic normal distribution (Text-fig. 4), perhaps indicating the spores were produced by a single population of one or only a few species.

TEXT-FIG. 4. Size frequency distribution of a hundred *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 from sample R 2, Rushbury (*ellesae* Graptolite Biozone); $\bar{x}$ = 27.9 μ m.



Genus SYNORISPORITES Richardson and Lister, 1969

Type species. *Synorisporites downtonensis* Richardson and Lister, 1969.

Synorisporites cf. *S.?* *libycus* Richardson and Ioannides, 1973

Text-fig. 3i, j

Figured specimens. FM 180, Text-fig. 3i, slide GL 22/1, 130 1030, sample ET 7a; FM 181, Text-fig. 3j, slide ET 8/3 180 1264, sample ET 6, both samples from the Eaton Track, upper Coalbrookdale Formation.

Description. Amb sub-triangular with convex sides and rounded apices. Distally originally elliptical in equatorial view with a flattened pyramidal proximal surface. Equatorial crassitude narrow, 0.5(1.5)3 μ m wide, and may be indistinct. Contact surface laevigate. Distal exine c. 1 μ m thick, sculptured with low, rounded and relatively broad muri and discrete verrucae or muri often composed of coalescent verrucae, 2(4)6 μ m long,

Limestone Formation, *ludensis* Graptolite Biozone. E, FM 176 (slide Rush Vill S1/3 co-ord 182 1223; E.F. no: S54/5/T54/2), sample R 2, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. F, FM 177 (slide ET 8/5, co-ord 130 1240; E.F. no: N54/4/054/2), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. G, FM 178 (slide Rush Vill S1/3 co-ord 180 1050; E.F. no: T35/2), sample R2, lower Coalbrookdale Formation, *ellesae* Graptolite Biozone. H, FM 179 (slide ET 8/5 co-ord 123 1380; E.F. no: N69/1), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. I, J, *Synorisporites* cf. *S.?* *libycus* Richardson and Ioannides, 1973. I, Tetrad; FM 180 (slide GL22/1 co-ord 130 1030; E.F. no: 032/2/4), sample ET 7a, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. J, isolated spore showing trilete mark; FM 181 (slide ET 8/3, 180 1264; E.F. no: S56), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. K, *Archaeozonotriletes chulus* (Cramer) var. *nanus* Richardson and Lister, 1969. FM 182 (slide S29/3 co-ord 040 0950; E.F. no: C23/2/C24/1), sample G 9, Buildwas Formation, *centrifugus* Graptolite Biozone. L, *Archaeozonotriletes chulus* (Cramer) var. *chulus* Richardson and Lister, 1969. FM 183 (slide ET 8/3 co-ord 225 1390; E.F. no: X69/X70), sample ET 6, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. M-O. MURORNATE TETRADS. M, FM 184 (slide ET 7/4 co-ord 150 1087; E.F. no: P38/4), sample ET 5, upper Coalbrookdale Formation, *lundgreni* Graptolite Biozone. N, FM 185 (slide ET 15/1 157 1312; E.F. no: Q61/2), sample ET 14, Farley Member, *ludensis* Graptolite Biozone. O, FM 186 (slide WL 2/5 co-ord 006 1364; E.F. no: A66), sample WL 2, lower Much Wenlock Limestone Formation, *ludensis* Graptolite Biozone.

1(2)5 μm wide, < 1 μm high and 0.5(1)4 μm apart. Trilete mark distinct, with straight to slightly sinuous sutures which extend to the equator or nearly so, and are accompanied by low lips, *c.* 1 μm high and wide.

Dimensions. Maximum diameter 18(26)32 μm (4 specimens measured).

Distribution. Upper Coalbrookdale Formation and lower Farley Member, upper *lundgreni* to lower *nassa* Graptolite Biozones.

Comparisons. *Synorisporites? libycus* Richardson and Ioannides, 1973 is of similar size (19–42 μm) but includes some spores with broader verrucae (2–8 μm). *S. verrucatus* Richardson and Lister, 1969 from the lower Downton Group (= Pridoli age) has smaller and more prominent verrucae.

TRILETE MIOSPORE type 1

Text-fig. 3A–C

Figured specimens. FM 172, Text-fig. 3A, slide Rush S10/4 135 1090, sample R 14, Rushbury Pack Track, upper Coalbrookdale Formation; FM 173, Text-fig. 3B, slide GL22/1 063 1048, sample ET 7a, Eaton Track, upper Coalbrookdale Formation; FM 174, Text-fig. 3C, slide ET 9A/1, 070 1145, sample ET 8, Eaton Track, Farley Member.

Description. Amb sub-triangular with convex sides and rounded apices. Equatorial crassitude narrow, 0.5–3.5 μm wide. Proximal surface sculptured with convolute and anastomosing muri *c.* 1 μm wide and 0.5 μm apart; muri are radially aligned near the equator but are predominantly randomly orientated over the remainder of the proximal surface. Distal exine *c.* 1 μm thick; laevigate in two specimens, and with scattered grana in one specimen.

Dimensions. Maximum diameter 28(35)40 μm (three specimens measured from samples ET 7c and ET 8).

Distribution. Upper Coalbrookdale Formation to lower Farley Member. Lower *nassa* Graptolite Biozone.

Comparisons. *Emphanisporites* McGregor, 1961 has proximal muri which are predominantly radial whereas in Trilete Miospore type 1 the muri are mainly randomly oriented.

Infraturma PATINATI (Butterworth and Williams) emend. Smith and Butterworth, 1967
Genus ARCHAEOZONOTRILETES (Naumova) Allen, 1965

Type species. *Archaeozonotriletes variabilis* (Naumova) Allen, 1965.

Archaeozonotriletes chulus (Cramer) var. *chulus* Richardson and Lister, 1969

Text-fig. 3L

Figured specimen. FM 183, Text-fig. 3L, slide ET 8/3, 225 1390, sample ET 6, Eaton Track, upper Coalbrookdale Formation.

Dimensions. Diameter 36(39)43 μm (17 specimens measured). Equatorial exine width 2–6 μm ; exine 1.5–4 μm thick at distal pole.

Distribution. Throughout the Wenlock, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparisons. The genus *Archaeozonotriletes* is preferred for these spores because the distal patina is either the same as, or similar in thickness to, the equatorial thickness (Table 2). *Tholisporites*

TABLE 2. Exine thickness in spores of the *Archaeozonotriletes chulus* var. *chulus* type from the Welsh Borderland (Richardson and Lister 1969).

	Distal pole	Equator	
		Inter-radial	Radial
Wenlock	1.5–4 μm	2–6 μm	?
Downton	4–5 μm	4–6 μm	3–6 μm
Ditton	2.0–2.5 μm	2.5–5 μm (3.5–4.5)	?

Butterworth and Williams, 1958 has a 'Patina thickest in the equatorial region, thinning slightly towards the distal pole.' Although Smith and Butterworth (1967) report a distal thickness for *T. scoticus* (the type species) 'usually less than the equatorial thickness', they compare *Tholisporites* with a cingulate genus *Densosporites*. Further, *A. chulus* (Cramer) is elliptical in equatorial view and usually preserved in polar compression whereas the type species of both *Tholisporites* and *Archaeozonotriletes* are more inflated, hemispherical in lateral view, and commonly compressed in lateral orientation (Allen 1965, p. 721; Smith and Butterworth 1967, p. 268). Thus *A. chulus* differs in basic shape/structure from both the genera with which it has been compared. The genus *Archaeozonotriletes* has priority over *Tholisporites* and it remains to be seen whether these two genera can be separated on a satisfactory basis and whether spores with a less inflated distal hemisphere should be accommodated in a new genus.

Remarks. JBR is a member of an international working group looking at species of the *chulus* type and pending its results we prefer to leave this species in the genus *Archaeozonotriletes*.

Archaeozonotriletes chulus (Cramer) var. *nanus* Richardson and Lister, 1969

Text-fig. 3k

Figured specimen. FM 182, Text-fig. 3k, slide S29/3, 040 0950, sample G 9, Hughley Brook, Buildwas Formation.

Dimensions. Diameter 21.5(28)35 μm (14 specimens measured from various samples); equatorial exine width 2–6 μm ; exine 1.5–4 μm at distal pole.

Distribution. Throughout the Wenlock, Buildwas to Much Wenlock Limestone Formations; basal *centrifugus* to lower *ludensis* Graptolite Biozones.

Comparison. A bimodal size distribution was demonstrated for the two varieties of *A. chulus* by Richardson and Lister (1969) for Upper Silurian (Downtonian) and Lower Devonian (Dittonian) specimens. The present work shows that in the lower Wenlock (Buildwas Formation) *A. chulus* var. *nanus* is dominant whereas *A. chulus* var. *chulus* dominates higher in the Wenlock.

INCERTAE SEDIS
MURORNATE TETRADS

Text-fig. 3M–O

Figured specimen. FM 184, Text-fig. 3M, slide ET 7/4, 150 1087, sample ET 5, Eaton Track, upper Coalbrookdale Formation; FM 185, Text-fig. 3N, slide ET 15/1, 157 1312, sample ET 14, Eaton Track, Farley Member; FM 186, Text-fig. 3o, slide WL2/5, 006 1364, sample WL 2, Harton Hollow Wood Quarry, lower Much Wenlock Limestone Formation.

Description. Tetrads of closely adherent spores with murornate sculpture. Individual spores with triangular to subtriangular amb. Proximal surface not seen. Distal exine sculptured with elongate, narrow (0.5(1)1.5 μm wide), sinuous to convolute and anastomosing, low ($< 1 \mu\text{m}$ high) and rounded muri; elements discrete but occasionally closely spaced, and fused, $< 0.5\text{--}3 \mu\text{m}$ apart.

Dimensions. Tetrads 31(38)50 μm in diameter; individual spores 21.5(31)36 μm in width (20 specimens measured).

Distribution. Upper Coalbrookdale Formation, Farley Member, and Much Wenlock Limestone; *nassa* to lower *ludensis* Graptolite Biozones.

Comparison. *Nodospora rugosa* Strother and Traverse, 1979 from the Llandovery of North America is a permanent cryptospore tetrad with superficially similar sculpture. However, in *N. rugosa* this sculpture is present on an envelope surrounding the cryptospore tetrad whereas in this species the spore exine is sculptured. Tetrads of rugulate trilete miospores would also appear similar, but one might expect to recover isolated miospores in the same samples; this has not occurred with this species. We are therefore unsure if these tetrads are cryptospores or the tetrads of trilete miospores and hence have included them under *Incertae sedis* pending further investigations.

COMPARISONS WITH OTHER ASSEMBLAGES

Most records of early sporomorphs and plant megafossils have come from Baltica (Britain, Scandinavia and European USSR, Livermore *et al.* 1985). Other sporomorph records for the Silurian come from Laurasia (USA) and Gondwana (North Africa and South America) but so far there are none from Australia, Siberia, Antarctica or China. Even fewer of these assemblages are represented by diverse microfloras (see Table 3).

BIOSTRATIGRAPHY

A spore zonal scheme for the Silurian and Devonian of the northern hemisphere has been proposed by Richardson and McGregor (1986). In this inter-regional scheme Wenlock strata encompass two assemblage biozones: the *chulus-namus* (Late Llandovery to Late Wenlock, Telychian to Late Homerian) and cf. *protophanus-verrucatus* (Late Wenlock and Early Ludlow, Late Homerian to Early Gorstian). In the Wenlock of the type area characteristic species of the cf. *protophanus-verrucatus* Biozone first appear in upper *lundgreni* Graptolite Biozone of the Eaton Track and Rushbury Pack Track sections (Text-fig. 5). Thus all the Sheinwoodian and lowermost Homerian probably belong to the *chulus-namus* Biozone. The nominal species of the upper zone are the hilate cryptospores, ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta* of this work) and cf. *Synorisporites verrucatus* (= *Hispanaediscus verrucatus* of this work). As a result of these new data, the base of the zone is redefined in the Eaton Track Section.

cf. *protophanus-verrucatus* Assemblage Biozone.

The new reference section for the base of this zone is defined in the Upper Coalbrookdale Formation of the type area of the Wenlock Series. The base is taken as sample ET 5 (approximately midway between localities 20 and 21 of Bassett *et al.* 1975) in the Eaton Track Section, of upper *lundgreni* Graptolite Biozone age. The nominal species ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta*) is rare at this horizon but both nominal species occur c. 4 m above in sample ET 6 (approximately locality 21 of Bassett *et al.* 1975) and become more common higher in the *lundgreni* Graptolite Biozone, sample ET 7a (locality 22 of Bassett *et al.* 1975), and above in the Eaton Track Section.

Remarks. In the Rushbury Pack Track, the nominal species cf. *Synorisporites verrucatus* (=

TABLE 3: Homeric and Sheinwoodian spores from the type Wenlock area and around the world

	Great Britain and Ireland (Baltica)					North Africa (Gondwana)			North America (Laurentia)	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
	HOMERIAN									
<i>Ambitisporites dilutus</i>	+	+	+	.	+	+	+	+	+	+
<i>A. avitus</i>	+	+	+	.	+	+	+	+	+	+
<i>Archaeozonotriletes chulus</i> var. <i>chulus</i>	+	-	-	.	+	-	+	-	-	-
<i>A. chulus</i> var. <i>nanus</i>	+	-	-	.	+	-	+	-	-	-
<i>Synorisporites</i> cf. <i>S. ? libycus</i>	+	?	-	.	-	-	+	-	-	-
Murornate tetrads	+	-	-	.	+	-	-	-	-	-
Trilete miospore type 1	+	-	-	.	-	-	-	-	-	-
<i>Enphanisporites protophanus</i>	-	-	-	.	-	-	+	-	-	-
<i>Laevolancis divellomedium</i>	+	+	+	.	+	-	+	+	-	+
<i>L. plicata</i>	+	-	-	.	-	-	-	-	-	-
<i>Artemiopyra brevicosta</i>	+	-	-	.	-	-	+	-	-	+
<i>A. sp. A</i>	+	-	-	.	-	-	-	-	-	-
<i>Hispanaedicus wenlockensis</i>	+	-	-	.	-	-	-	-	-	-
<i>H. verrucatus</i>	+	-	-	.	+	-	+	-	-	+
cf. <i>H. sp. A</i>	+	-	-	.	-	-	-	-	?	-
Hilate cryptospore type 1	+	-	-	.	-	-	-	-	-	+
<i>Dyadospora murusattenuata</i>	+	-	-	.	-	-	-	-	-	+
<i>D. murusdensa</i>	+	-	-	.	-	-	-	-	-	+
<i>Tetrahedraletes medinensis</i>	+	-	-	.	-	+	-	-	-	.
	SHEINWOODIAN									
<i>Ambitisporites dilutus</i>	+	+	.	+	.	+	.	.	.	.
<i>A. avitus</i>	+	+	.	-	.	+	.	.	.	.
<i>Archaeozonotriletes chulus</i> var. <i>chulus</i>	+	-	.	-	.	-	.	.	.	.
<i>A. chulus</i> var. <i>nanus</i>	+	-	.	-	.	-	.	.	.	.
<i>Laevolancis divellomedium</i>	+	+	.	-	.	-	.	.	.	.
<i>L. plicata</i>	+	-	.	-	.	-	.	.	.	.
<i>Dyadospora murusattenuata</i>	+	-	.	-	.	-	.	.	.	.
<i>D. murusdensa</i>	+	-	.	-	.	-	.	.	.	.
<i>Tetrahedraletes medinensis</i>	+	-	.	-	.	-	.	.	.	.

(1) This study; (2) Downie (1963); (3) Dornig (1981b, 1983); (4) Mabillard and Aldridge (1981); (5) Richardson and Lister (1969); (6) Smith (1979); (7) Richardson and Ioannides (1973)†; (8) Magloire (1968)†; (9) Jardine and Yapaudjian (1968)†; (10) Strother and Traverse (1979)†*.

* Assessment of species not described by Strother and Traverse is by personal observation of paratype material in the BM(NH) by N.D.B.

† Studies with poor dating.

. Strata not studied.

Hispanaedis discus verrucatus) occurs in sample R17 (approximately locality 44 of Bassett *et al.* 1975). This sample is also from the upper *lundgreni* Graptolite Biozone and is probably at a similar horizon to the Eaton Track Reference Section occurrences, but may be slightly lower. The Eaton Track is preferred as the zonal reference section because the spore record is better there. A single specimen of Trilete Miospore type 1 was also found in sample R14, approximately equivalent to locality 38 of Bassett *et al.* (1975) in the upper *lundgreni* Graptolite Biozone. This specimen represents the oldest sculptured miospore dated independently by graptolites.

Further zonal refinement may be possible, at least in the Anglo-Welsh Area. For example, the presence of *Artemopyra brevicosta* appears to be a good, though possibly only local, marker for the upper *lundgreni* to lower *nassa* Graptolite Biozones in that it has not yet been found from the later *nassa* or *ludensis* Biozones. Also, cf. *Hispanaedis discus* sp. A was not recorded in samples from the upper *lundgreni* Graptolite Biozone but is increasingly common in samples from the *nassa* and lower *ludensis* Biozones. Thus with further work this species may prove to be a useful indicator for the later Homeric. In the Libyan borehole sequences the miospore *Emphanisporites protophanus* appears higher in the sequence than ?*Emphanisporites* cf. *protophanus* (= *Artemopyra brevicosta*) but has not been found in the type Wenlock sequence examined. The first appearance of *E. protophanus* is placed in the overlying *libycus-poecilomorphus* Miospore Biozone by Richardson and McGregor (1986) and may prove to be an indicator of the latest Homeric or earliest Gorstian.

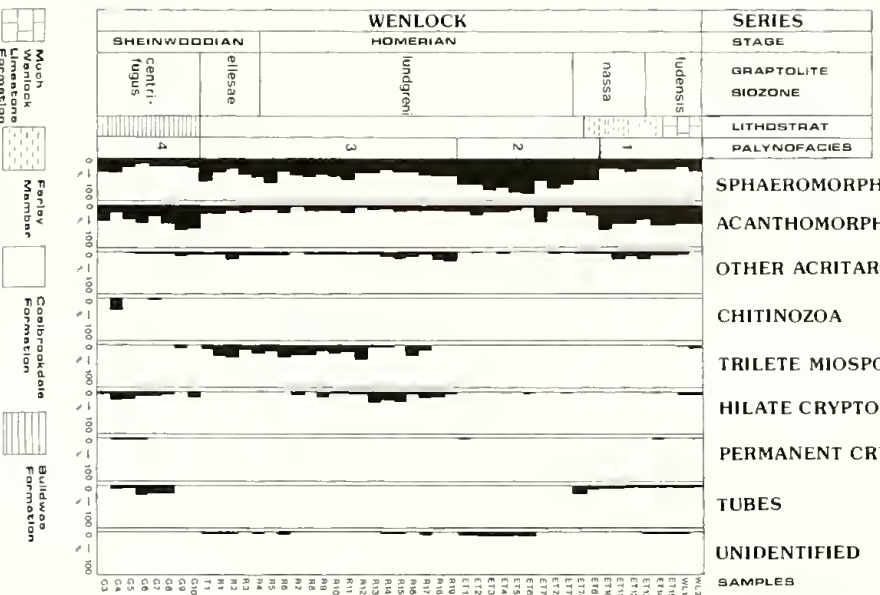
PALYNOFACIES

The appearance of sculpture on hilate cryptospores and trilete miospores is an event of biostratigraphical, biological and evolutionary significance. This event is useful for interregional stratigraphical correlation, and may relate to the primary diversification of land plants (rhyniophytoids). Consequently it is important to ascertain if the appearance of sculptured sporomorphs in the late *lundgreni* Graptolite Biozone of the type Wenlock area is a true 'evolutionary event' representing the first appearance of sculptured miospores and hilate cryptospores, or whether it is a preservational or depositional artifact. Several aspects of marine environments may be determined by studying the types and abundance of marine phytoplankton on the one hand and amounts of land-derived sporomorphs on the other. To this end organic-walled microphytoplankton (prasinophycean cysts and acritarchs), cryptospores and miospores, and organic-walled tubes (Burgess and Edwards in press) were counted from all samples, and used to produce a palynofacies profile of the sequence (Text-fig. 6).

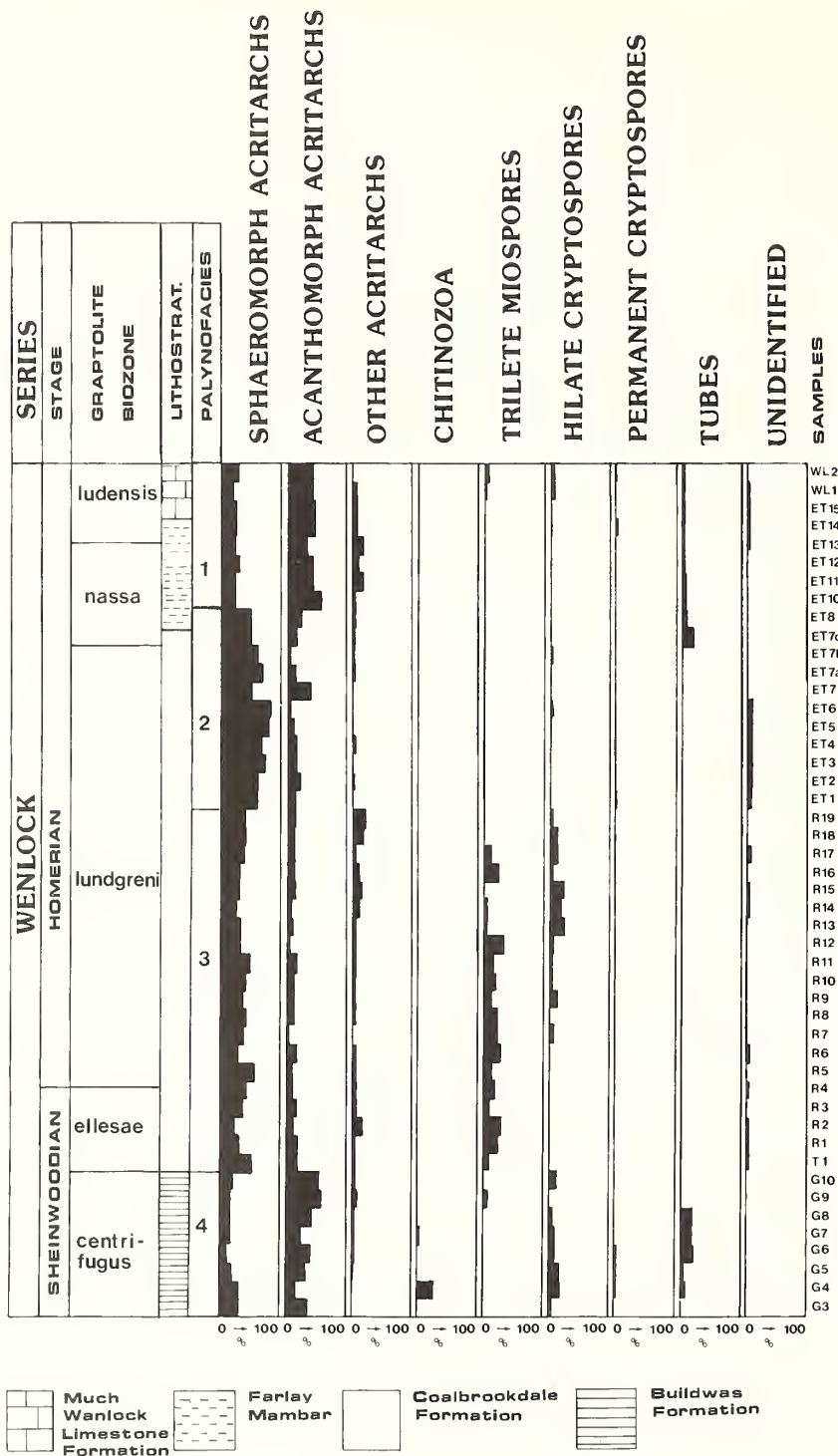
The assemblages of palynomorphs and fragments of plant megafossils recognized fall into four distinct palynofacies, which can be related to changes in the depositional environment and the first appearance of sculptured sporomorphs.

Palynofacies 4 was recorded from samples of the Buildwas Formation in the Hughley Brook Section. The predominant palynomorphs are acanthomorph acritarchs (15–55%) but there are also significant numbers of hilate cryptospores (5–10%) and tubes (up to 15%); trilete spores are rare (< 1%). Using existing palynofacies models, the Buildwas Formation samples appear to have been deposited in an offshore shelf environment with significant terrestrial input (Dorning 1981a; Al-Ameri 1983; Burgess 1987; Richardson and Rasul 1990). Sculptured palynomorphs were not recovered from this palynofacies.

Palynofacies 3 was recorded from samples of the Coalbrookdale Formation from sections around Rushbury. The assemblages are composed predominantly of prasinophyceae (sphaeromorph acritarchs) (30–55%), trilete miospores (up to 20%) and, near the top of the section, hilate cryptospores (up to 20%). Studies of Recent Sediments (Muller 1959) show that the proportion of land derived sporomorphs normally increases shorewards. In addition the proportion of prasinophycean 'phycomata' increases relative to acritarchs in inshore environments (Richardson and Rasul 1990). Thus the palynofacies indicates a shoreward shift in the environment of deposition. In contrast macrofossil studies (Bassett and Cocks pers. comm.) indicate that these beds were deposited in offshore shelf environments. Despite the common occurrence of sporomorphs in



TEXT-FIG. 6. Composition of palynological assemblages (%) through the type Wenlock area and the stratigraphical distribution of four palynofacies



TEXT-FIG. 6. Composition of palynological assemblages (%) through the type Wenlock area and the stratigraphical distribution of four palynofacies.

this palynofacies (up to 25% of the assemblage) sculptured specimens are rare with only two specimens being recovered towards the top of the sequence (Text-fig. 5).

Palynofacies 2 typifies the Coalbrookdale Formation of the Eaton Track Section and is characterized by a dominance of sphaeromorph acritarchs (50–90%). Acanthomorph acritarchs are considerably less abundant (5–25%) and sporomorphs are relatively rare (0–2%). Using our palynofacies model, this palynofacies represents the most distal phase of sedimentation in the type area and probably the deepest water, but it is within this part of the succession that sculptured sporomorphs become increasingly common (though < 1% of the assemblage).

Palynofacies 1 typifies the upper part of the Coalbrookdale Formation, Farley Member and lower Much Wenlock Limestone Formation of the Eaton Track Section and Harton Hollow Wood Quarry. This palynofacies is dominated by acanthomorph acritarchs (40–60%), with prasinophycean 'phycomata' (20–30%) and increased percentages of sporomorphs (0–3%) and tubes (5–10%). This palynofacies indicates an outer shelf environment and nearer to the shore than that indicated by Palynofacies 2. Sculptured sporomorphs become increasingly diverse through this part of the sequence but are still rare (< 1% of the total assemblage).

These palynofacies studies show that sporomorphs are most abundant in the late Sheinwoodian and early Homerian (*ellesae* to late *lundgreni* Graptolite Biozones) where they were all laevigate. The earliest sculptured sporomorphs found are from the late *lundgreni* Zone where the palynofacies indicates deposition in offshore, deeper water, environments and where sporomorphs are rare and generally form < 1% of the assemblage. Sculptured sporomorphs become increasingly diverse in samples from the upper most *lundgreni* to lowermost *ludensis* Zones, where palynofacies studies indicate deposition in slightly more proximal, but still offshore, shelf environments and sporomorphs form only around 1% of the assemblage. In conclusion, the appearance of sculptured sporomorphs in the late *lundgreni* Graptolite Biozone of the Wenlock Type Area does not appear to have been caused by a change in the depositional environment to a more proximal one, but appears to be a true event. Sediments from inshore environments would yield larger numbers of sporomorphs but would not be expected to affect the horizon of this event substantially.

DISCUSSION AND PALAEOBOTANICAL SIGNIFICANCE

Trilete miospores of the genera *Ambitisporites* and *Synorisporites* have been recorded in situ from specimens of *Cooksonia pertoni* in the Upper Silurian (Fanning *et al.* 1988). These spores are comparable to some of the dispersed miospores described above and indicate that similar rhyniophytoid plants may have been present in the Wenlock. The increasing diversity of trilete miospores noted from the late *lundgreni* Graptolite Biozone, especially the appearance of sculpture, strongly suggests that such plants began to diversify in the Homerian. The studies of Fanning *et al.* (1988) on *Cooksonia pertoni* indicate that some of these plants, although they produced both laevigate and sculptured spores, may have looked remarkably similar and the main differences between them may have related to characters of their spores.

The derivation of hilate cryptospores is poorly known. However, smooth-walled hilate cryptospores have been recorded from *Salopella*-like sporangia in the Lower Devonian (Fanning *et al.* in press) and the distribution of these spores shows that they were undoubtedly produced by land-plants. Hilate cryptospores are found throughout the Wenlock of the type area but the first sculptured species occur in the upper *lundgreni* Graptolite Biozone, at a similar horizon to the first sculptured trilete miospores. Thus the evidence from the hilate cryptospores also suggests that the late Wenlock was a time of major importance in the diversification of early land-plants.

Only one species of 'permanent' cryptospore tetrad (*Tetrahedraletes medinensis*) was recovered from the type Wenlock area. It ranges throughout the sequence and represents the youngest published record of the group (Gray 1985). They are also present in strata from the Rumney Inlier of South Wales which ranges from late Wenlock through to the early Downtonian (= Pridoli) (Burgess 1987), and J.B.R. (unpublished) has recorded them in studies of the Downtonian and Dittonian of the Welsh Borderland. However, higher in the sequence they are erratic in their

distribution, usually rare, and therefore may be reworked. The type(s) of plants producing these enigmatic palynomorphs are unknown although Gray (1985) has suggested that they may have been similar to some extant hepatics. The nature of the record of 'permanent' cryptospore tetrads in this study indicates that their parent plants were still extant in the Wenlock although their diversity had greatly declined when compared with early Llandovery assemblages (Burgess 1991).

Smooth-walled and internally thickened tubes (Burgess and Edwards in press), which may represent the remains of nematophytalean land plants have also been recovered throughout the sequence in the type Wenlock area. In addition, unornamented cuticles (*sensu* Edwards 1982), believed to form part of the nematophytalean land-plant *Nematothallus* Lang, also occur throughout the succession. The Wenlock records suggest to us that nematophytalean plants and possible nematophytalean, tube-bearing plants were widespread at this time but the nature of any contained spores remains unknown.

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A NEW MARSUPIATE CIDAROID ECHINOID FROM THE MAASTRICHTIAN OF ANTARCTICA

by DANIEL B. BLAKE *and* WILLIAM J. ZINSMEISTER

ABSTRACT. *Almucidaris durhami* is a new genus and species of cidaroid echinoid from the Maastrichtian (Late Cretaceous) of Seymour Island, Antarctic Peninsula. The species is unique in that the genital plates of the female are expanded and hollowed to form marsupia. The incidence of brooding in invertebrates, including echinoderms, increases with latitude and apparent stress; stressful conditions might have contributed to the evolution of *A. durhami*.

SEYMOUR Island, in the Antarctic Peninsula, has been the source of an extraordinary diversity of superbly preserved late Mesozoic and early Cenozoic fossils (Feldmann and Woodburne 1988). None of these many fossils is better preserved or more elegant than a specimen of the new cidaroid echinoid described here; the new species is important for more than the aesthetic value of its holotype, however, because the genital plates of the female were much enlarged to form deep brood chambers. Taxonomically diverse brooding echinoids, including cidaroids, are known from numerous other occurrences, and these shed some light on the evolution of brooding in *Almucidaris durhami* gen. et sp. nov.

BROODING IN ECHINOIDS

The biology of brooding in echinoderms was reviewed by Lawrence (1987), and a taxonomic survey of brooding echinoids was provided by Philip and Foster (1971). Lawrence (1987, p. 264) defined brooding as '... the association of embryos and juveniles with an adult, usually the female parent'. The definition is broad, and includes simple presence of the juveniles on the surface of the parent, without structural differentiation. Brooding increases probability of offspring survival at a cost of decreased fecundity and dispersal, and increased reproductive effort. Although brooding has been reported from all living echinoderm classes (except the Concentricycloidea), it is not common, indicating that costs tend to outweigh benefits. In echinoids, brooding always is external, with the young present either in marsupia or distributed among the spines without parent structural differentiation.

Within echinoderms, brooding is found in different trophic groups, but as with marine invertebrates in general, it increases with latitude. Seventeen of the eighteen known species of Antarctic echinoids are brooders (Magniez 1983), some occurring intertidally on subantarctic islands under conditions of considerable physical stress (Lawrence 1987). Brooding also is known from lower latitudes; Gladfelter (1978) described it in the shallow-water infaunal Caribbean cassiduloid *Cassidulus caribbearum*, for example. The test of *C. caribbearum* is unmodified and the young are carried among the aboral spines.

Barker (1985) studied reproductive behaviour in the modern brooding cidaroid *Goniocidaris umbraculum* from the deep (95 m) continental shelf off New Zealand. Laboratory studies showed that brooding in this species begins with the urchins partially burying themselves in bryozoan shell debris. Oocytes are passed along the ambulacra by means of ciliary and tube foot action from the gonopore to the peristomial region. The oocytes are buoyant, and both their buoyancy and the oral spines help hold as many as 60 oocytes at the peristome. After 47–55 days, juveniles begin to migrate from the peristome to the bases of the spines on the oral side of the adult. Field data suggest the

annual breeding cycle takes place over nearly a six month period, with juveniles remaining with the parents for approximately four months. The smallest individuals recovered with juveniles were under 18 mm in diameter.

Associated juveniles can be quite numerous; Magniez (1980) found the mean egg and juvenile number per female to be 27.3, with a maximum of 109, in a population of 315 females of the schizasterid spatangoid *Abatus cordatus* from Kerguelen Island.

Barker (1985) found controlling factors on brooding to be uncertain in *Goniocidaris*, which has a well defined annual breeding cycle. He suggested that photoperiod or nutrient accumulation might be important but that bottom temperature showed only a relatively minor 4 °C range of variation. This author further noted that the urchins do not feed during brooding; movement of the lantern might be sufficient to dislodge the eggs from the peristome. Partial burial might reduce risk of egg loss as well as provide a stable environment for the young. The range of *G. umbraculum* partially overlaps that of the broadcast spawning euechinoid *Pseudechinus huttoni* and both graze on the bryozoan *Cinctipora elegans*; however, competition was concluded not to have been involved with brooding in *G. umbraculum* because of the limited overlap of ranges. Hendler and Franz (1982) suggested brooding in the asteroid *Leptasterias* is a cold adaptation and not a result of competition; Barker (1985) preferred a temperature hypothesis for the origin of brooding in *G. umbraculum*.

Several living brooding cidaroids, including *Goniocidaris corona* (Barker 1968), *G. umbraculum* (D. L. Pawson pers. comm.), and *Austrocidaris canaliculata* (Philip and Foster 1971) carry young around the apical system; juveniles of other species are found at the peristome, protected by the primary spines. In *Austrocidaris*, a sunken median furrow is present in both ambulacra and interambulacra, and young can cling to the apical surface. The enlarged genital-plate marsupia of *Almucidaris* gen. nov. are unique.

De Ridder and Lawrence (1982) reviewed the literature on food resources of echinoids; available data on cidaroids were largely drawn from Mortensen (1928), whose observations were based primarily on gut contents. Cidaroid food consists of a diversity of bottom materials, including foraminifers, bryozoans, sponges and other generally smaller particles.

STRATIGRAPHIC OCCURRENCE OF *ALMUCIDARIS DURHAMI*

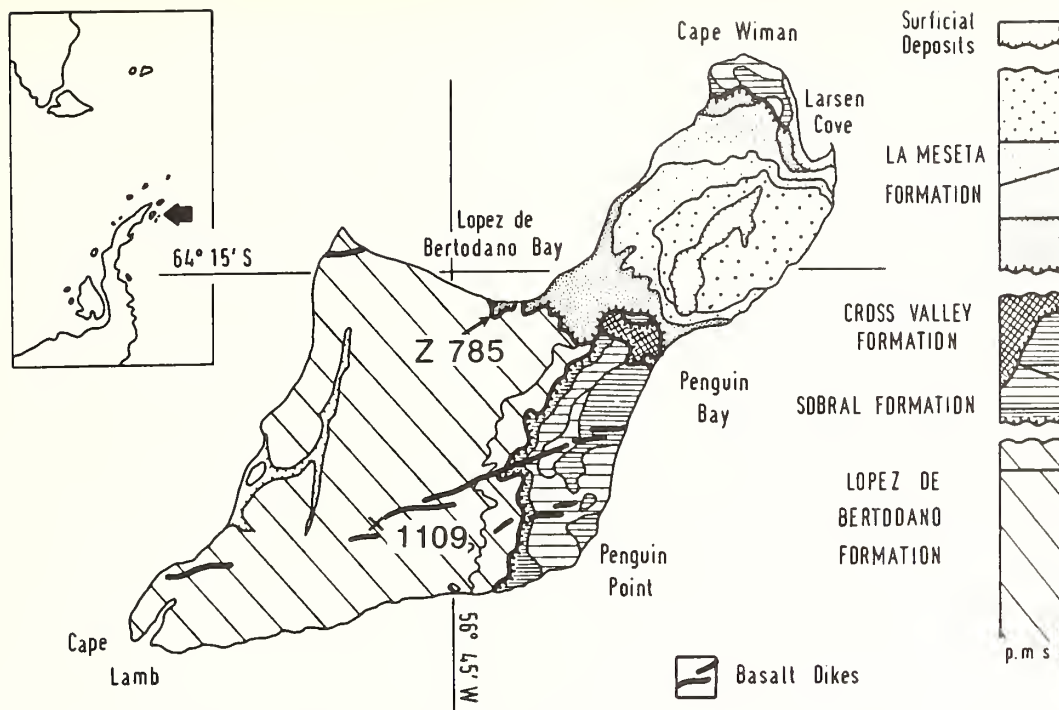
The holotype was collected from the Maastrichtian portion of the Lopez de Bertodano Formation of Seymour Island, Antarctic Peninsula (Text-fig. 1). The formation consists of approximately 1200 m of sandy siltstones and siltstones with numerous concretionary horizons. Although the invertebrate fauna is moderately diverse and well preserved, the abundance of individuals within any given interval is not great. Fragmentary echinoid material is abundant at a number of horizons; however, the holotype is the only known complete individual.

The specimens of *Almucidaris durhami* gen. et sp. nov. were collected from a 25 m interval of medium grey siltstone 320 m below the K/T boundary. Extensive bioturbation characterized by *Bergaueria* and Phycodes-like structures have destroyed all primary bedding structures. The absence of any primary sedimentary structures and the intensely bioturbated nature of the sediments suggest that the environment of deposition of this horizon was below wave base in a mid or outer shelf setting.

Although the fossils from the siltstone are not abundant, the fauna is exceptionally diverse (35 taxa) for the Lopez de Bertodano Formation, and remarkably well preserved. The composition of the invertebrate fauna from this siltstone interval differs markedly from that of the rest of the Lopez de Bertodano Formation by the presence of a large number of small gastropods that have not been encountered elsewhere in the formation. The molluscan fauna from the Antarctic Cretaceous generally is characterized by relatively large, thick-shelled species; the occurrence of many small, thin-shelled taxa indicates an unusual local facies not seen elsewhere in this unit.

BROODING IN *ALMUCIDARIS DURHAMI*

Although a number of aboral brooders are known among echinoids, peristomial brooding is



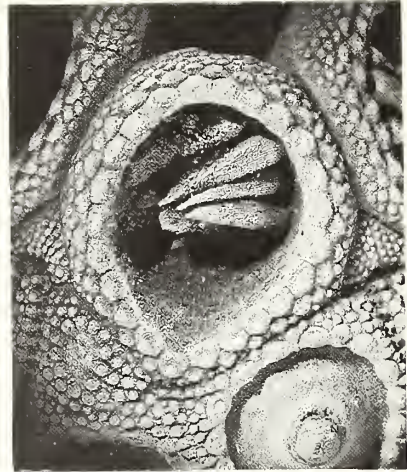
TEXT-FIG. 1. Geological locality map of Seymour Island, Antarctic Peninsula. The Lopez de Bertodano Formation is Cretaceous and Paleocene; that part of it in which the echinoid material was found is Maastrichtian. The Sobral and Cross Valley Formations are Paleocene, and the La Meseta is Eocene in age.

dominant; the latter provides more protection, but probably interferes with the parent's feeding. In contrast, the genital-plate marsupia of *A. durhami* (Text-fig. 2) provided effective protection yet they would not have impaired feeding. A second advantage of brood chambers in the genital plates was that oocytes could be transferred from the interior to them with little chance of loss. Many echinoid marsupia are formed by depressions in the test, and although all marsupia in echinoids are topologically external, they can utilize a significant percentage of the volume of the interior; the raised marsupia of *A. durhami* provided enclosed space without decreasing the parent's internal volume.

Almucidaris durhami, like *Goniocidaris umbraculum*, apparently lived below wave base, and therefore the adaptive value of marsupia in *A. durhami* was not directly related to variation in shallow-water conditions, although as in *Goniocidaris*, perhaps availability of nutrients was important.

Size at which juveniles become independent varies among species, but space is quite limited within the marsupia of *A. durhami*. Barker (1985) illustrated juveniles of *G. umbraculum* clinging to the spines of the adult; these had a test diameter of about 3 mm, and diameter including spines was approximately 6 mm. Perhaps juveniles of *A. durhami*, like those of *G. umbraculum*, moved onto the spines of the adult during ontogeny, freeing marsupial space for younger individuals. Sequentially overlapping broods are known in *Cassidulus caribbearum* (Gladfelter 1978).

Cidaroid taxonomy has proven difficult, in part because of individual variation and lack of agreement on phylogenetically significant characters. Smith and Wright (1989) provided a historical survey of cidaroid taxonomy, a revised classification, and a phylogenetic reconstruction. Their system is followed here, along with the taxonomic treatment of Philip (1963, 1964).



TEXT-FIG. 2. *Almucidaris durhami* gen. et sp. nov., holotype USNM 446322, two marsupia with spines displaced from scrobicular rings into the chambers, both $\times 6$.

SYSTEMATIC PALAEOLOGY

Class ECHINOIDEA Leske, 1778
 Order CIDAROIDA Claus, 1880
 Family CIDARIDAE Gray, 1825
 Subfamily CIDARINAE Gray, 1825
 Tribe CIDARINI Gray, 1825
 Genus ALMUCIDARIS gen. nov.

Type species. *Almucidaris durhami* sp. nov.

Etymology. Almus (L.); fostering, nourishing, cherishing; in reference to the brooding behaviour.

Diagnosis. Cidariniid with large genital plates forming deep marsupia, at least in females; ambulacral column pore rows strongly sinuous; podial pairs inclined perradially, not conjugate; interambulacral plates of adult with densely arranged tubercles, plate sutures closed by tubercles.

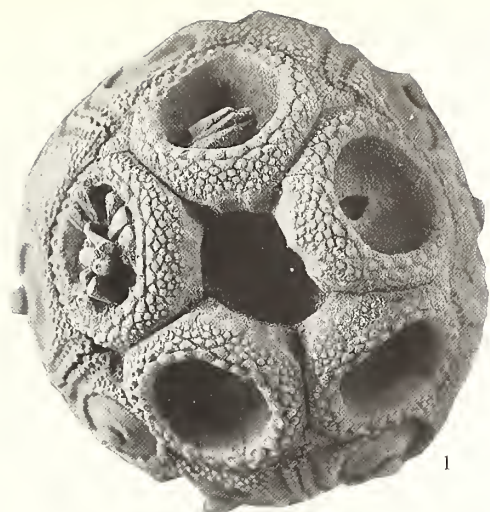
Almucidaris durhami sp. nov.

Plate 1, figs 1–6; Text-fig. 2

Material. Available material consists of one complete test (holotype, United States National Museum [USNM] 446322), the base of a second, and 25 test fragments, the latter ranging from single plates to nearly complete interambulacra with portions of adjacent ambulacra (paratypes USNM 446323–446348). Small spines are associated with the complete specimen and the base. Four isolated marsupial plates are included among the 25 fragments. Maastrichtian, Upper Cretaceous, Seymour Island, Antarctic Peninsula.

EXPLANATION OF PLATE I

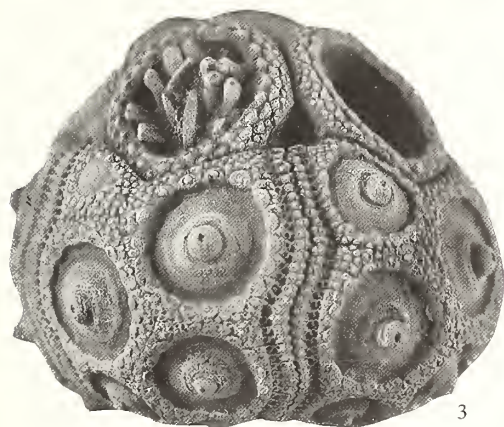
Figs 1–6, *Almucidaris durhami* gen. et sp. nov., holotype, USNM 446322, Maastrichtian, Seymour Island, Antarctic Peninsula. 1, aboral view, note large facets for periproctal plates, gonopore, and spines collapsed into marsupia, $\times 2$. 2, ambulacral detail, $\times 6$. 3 and 4, stereo pair, lateral views, $\times 2$. 5, oral view, $\times 2$. 6, ambulacral detail, specimen is partially separated along perradial suture, $\times 6$.



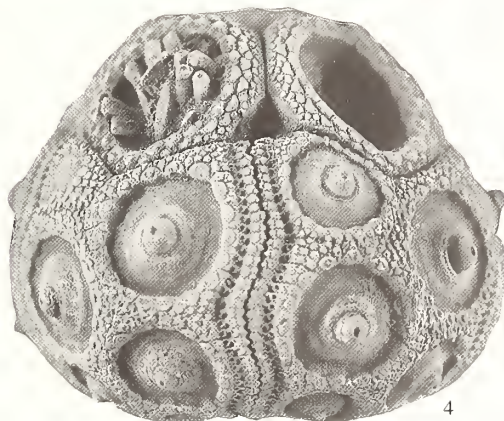
1



2



3



4



5



6

Etymology. The species is named in honour of Dr J. Wyatt Durham.

Diagnosis. As for the genus.

Description. The diameter of the holotype is 35 mm and the height is 21 mm; the height of the corona and genital ring together are 30 mm. The corona is somewhat flattened, with the apical ring forming a prominent, peaked aboral profile. The periproctal outline is elongate pentameral, with a length of 9 mm and a breadth of 7 mm; all periproctal plates were lost but large articular surfaces on the genital plates demonstrate that periproctals were large. The genitals are much enlarged, approximately 14–15 mm (vertical dimension) by 13–14 mm. They contain open hemispherical marsupial chambers which are approximately 10 by 8.5 mm; chamber openings are directed laterally and aborally. A genital pore is present at the base of each chamber; it is approximately 2 mm in length. The outer surface of the genital plate is covered by closely spaced tubercles which diminish in size away from the enlarged scrobicular ring; the scrobicular ring and the next lateral ring have rounded crescentic depressions which are directed toward the chamber, thus allowing spines to be deflected over the chamber opening. Oculars are triangular but indented at their bases; their breadth is approximately 4 mm and height is 3.5 mm. Oculars are covered by closely spaced tubercles of uniform size. Apical ring plate boundaries are incised and they are neither pitted nor have areas bare of tubercles. Ambulacra are strongly sinuous throughout. Ambulacral width at the ambitus is 10–11% of test diameter, with the combined pore zones forming nearly one-half of the ambulacral width. Ambulacral pores are uniserial and pairs are inclined, with the perradial member of the pair lower than the adradial. Pores are not conjugate; the interporal partition is slightly broader than the width of a single pore. A clearly defined furrow extends from below the perradial pore to the lower edge of the ossicle; the groove is gradually lost toward the adradial pore. The perradial end of the plate has a single enlarged tubercle occupying the full plate height; one or two vertically aligned smaller perradial tubercles also are present, and on some ossicles, one or two additional small miliary tubercles are fitted among the perradial series. Most tubercles other than those of the enlarged series are absent near the peristome and periproct. Perradial sutures are not bare or pitted. Each interambulacral column consists of four or five plates, and all but perhaps one or two of the most recently-added plates have functional tubercles. The height and width of the plates are approximately equal, or the width is the slightly greater dimension. Primary tubercles are large with areoles of only the smallest adoral plates being confluent. The scrobicular series of slightly larger plates are tangent; plates ambitally and adapically in the series have closely arranged miliary tubercles separating the neighbouring scrobicular series. Sutural boundaries are not incised or bare, although scattered small pits are present. Areoles are deeply incised, occupying approximately 75% of the plate width at the ambitus. Mamelon diameter is 15–20% of plate width and most are perforate, although some adoral mamelons are imperforate or their condition was not preserved; they are weakly crenulate. Scrobicular tubercle series are clearly enlarged, with a distinct mamelon and a small crescentic depression toward the areole. Peristomial diameter is approximately 40% of test diameter; the lantern is unknown. Spines of genital plates are cuneate in cross-section, and therefore they were closely fitted in life; they have longitudinal beaded ribbing.

Available isolated coronal fragments and plates (paratype specimens) add relatively little, in part because the surfaces of most have been abraded by wind and dust. The largest interambulacral plate is 19 by 13 mm, and that of an ambital interambulacral plate on the holotype is 11 by 10 mm, suggesting plate growth was anisometric. If test diameter was proportionate to ambital plate width, a diameter of at least 60 mm was attained. One adoral plate has a clearly crenulate tubercle. Although isolated, four marsupiate genitals were recovered, but no dimorphic examples were found. A basal test fragment retains a number of cuneate scrobicular spine fragments similar to those of the genitals, again indicating a closely fitted, protective arrangement.

Remarks. *Almucidaris* is assigned to the Cidarinae (sensu Smith and Wright 1989) based on the presence of well defined perforate tubercles; it is assigned to the Cidarini based on presence of well developed adapical tubercles and the presence in adults of tubercles obscuring plate sutures, and weakly developed sutural pits. Positive evidence on subtribal affinities is lacking, although pore pairs are neither conjugate or subconjugate and therefore *Almucidaris* does not belong to the Phylacanthina. Smith and Wright (1989) noted that although the Cidarini is distinguished by pedicellariae and intestinal plate characters not found in fossils, some constituent genera can be traced back to the Lower Cretaceous; *Almucidaris* is similar to such genera as *Prionocidaris* sensu Smith and Wright (1989), and *Phylacanthus* sensu Philip (1963). It differs from both in the nature

of the pore pairs, and from the latter in the nature of the scrobicular spine bases (less strongly differentiated in *Ahmucidaris*) and the presence of marsupia. It is unlike *Prionocidaris* (but similar to *Phyllacanthus*) in the development of test tubercles.

Acknowledgements. The discovery of the holotype of *Ahmucidaris* would not have been possible without the generous field support provided by Dr Carlos Rinaldi, director of the Instituto Antartico Argentino, during the austral summer of 1988–1989. Field work was supported by Division of Polar Programs grant no. DPP 8416783 to W.J.Z. D. L. Pawson and A. B. Smith reviewed and provided numerous useful suggestions on an earlier version of the manuscript.

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A NEW SPECIES OF MACHAERIDIAN FROM THE SILURIAN OF PODOLIA, USSR, WITH A REVIEW OF THE TURRILEPADIDAE

by J. M. ADRAIN, B. D. E. CHATTERTON and L. R. M. COCKS

ABSTRACT. Machaeridians are enigmatic marine fossils, known from rocks of Ordovician to Carboniferous age. *Turrilepas modzalevskae* sp. nov., from Podolia, Ukraine, USSR, is only the second turrilepadid machaeridian species to be represented by an articulated assemblage. It provides unequivocal evidence for the presence of minute marginal spines, and demonstrates the relationship between these spines and the ornament of the outer sclerite surface. A standardized system of terminology for turrilepadid machaeridians is presented, based on examination of many specimens of *Turrilepas wrightiana* (de Koninck) from the Wenlock of Britain, together with undescribed Canadian silicified material. The anterior structure of turrilepadids and plumulitids is very similar, both lacking outer series sclerites on the first two segments. The Family Turrilepadidae comprises the genera *Turrilepas* Woodward, *Deltacoleus* Withers, *Clarkeolepis* Elias, *Spinacoleus* Schallreuter, and *Mojzsalepis* Dzik. All but *Turrilepas* are inadequately known.

DURING a visit to the Natural History Museum in 1988, J.M.A. discovered a specimen in the palaeontological collections labelled *Lepidocoleus* sp., collected from Podolia in 1983 by L.R.M.C. It was recognized that the specimen belonged in fact to *Turrilepas* Woodward, 1865, and was important because it represented only the second unequivocal record of the genus. The type species is from the British Wenlock.

Turrilepas modzalevskae, described herein, is only the second turrilepadid species to be represented by an articulated specimen. Examination of the many specimens of *Turrilepas wrightiana* in the Natural History Museum, together with knowledge derived from study of undescribed North American silicified faunas by J.M.A. has resulted in a more thorough understanding of the arrangement and structure of the turrilepadid scleritome, a subject to which little new information has been added since T. H. Withers's seminal work of 1926. An attempt is made to standardize descriptive terminology, and the status of the currently recognized turrilepadid taxa is reviewed. A historical review of machaeridian study and a discussion of recent systematic problems is presented elsewhere (Adrain in press). Illustrations of silicified sclerites are scanning electron micrographs. Illustrated calcareous specimens were blackened and given a light coating of ammonium chloride sublimate prior to photography. Illustrated specimens are housed in the Natural History Museum, prefixed BM(NH), and the palaeontological collections of the University of Alberta, prefixed UA.

LOCALITY AND STRATIGRAPHY

Podolia lies in the centre of eastern Europe; until the Second World War it was in Poland and since then it has formed part of the Ukraine. Access has been difficult, but in May 1983 the Silurian Subcommittee was invited to visit and collect from the sequence, which consists of nearly flat-lying beds of mostly late Silurian and early Devonian age all unconformably overlain by the Cretaceous (Koren *et al.* 1989). The locality of the new species of *Turrilepas*, *T. modzalevskae*, lies in a natural outcrop on the left slope near the mouth of the Smotrich River, near Tsvicklevtsy village (Tsegelnjuk *et al.* 1983, Stop 4, p. 75). Here the Ustje Member of the Bagovitsa Formation is exposed to 9.5 m and overlain conformably by Konovka Formation, which is composed of a lower

Goloskov Member (11.5 m) and an upper Shutnovsky Member (17.9 m), in turn overlain by the Sokol Member of the Tsvicklevtsy Formation which is seen to 19 m. The new *Turrilepas* undoubtedly came from the Konovka Formation, but since the single specimen was found loose, it is uncertain whether it came from the Goloskov or the Shutnovsky Member. Both members yield a very similar shelly fauna dominated by the brachiopods *Atrypella*, *Microsphaeridiorhynchus*, *Protochonetes*, and *Sphaerirhynchia*, and in other accounts (e.g. Koren *et al.* 1989) the members are not used. The age of the Konovka Formation is also securely fixed as basal Ludlow (lower Gorstian Stage), based not only on the brachiopods, but also on the ostracods present (Koren *et al.* 1989, fig. 108); however, there are no useful records of graptolites from that part of the Podolian succession.

TERMINOLOGY

There is no standard system of terminology for description of machaeridian sclerites and sclerite assemblages, although Jell (1979) and Schallreuter (1985) have made progress. Withers (1926) provided a comprehensive set of terms. His opinion was, however, that machaeridians were sessile, attached to the substrate by one end of their assemblage, and capable of opening and closing their assemblage along what he termed the 'free margin'. This interpretation of function and orientation now seems highly improbable (Jell 1979; Schallreuter 1985; Dzik 1986), and hence Withers's descriptive terms are largely obsolete. It is now generally accepted that machaeridians were vagile, that the more modified end of their assemblages was anterior, with the sclerites imbricating posteriorly, and that the median line along which opposing series sclerites meet in all known machaeridians was dorsal.

This orientation is followed here, but problems arise when comparing isolated sclerites, as homologous parts may be held in completely different orientations in the assemblages of different machaeridians. Furthermore, there is often sufficient serial variation along the scleritome that anteriorly placed, midbody, and posteriorly placed sclerites will have different orientations with respect to the general orientation of the whole assemblage. It has therefore been found necessary to adopt conventions when referring to particular aspects of sclerites. These conventions follow from the most general orientation of the sclerite and facilitate comparisons between differently arranged taxa, but do not necessarily correspond to what would have been the actual orientation of the part in a particular living machaeridian.

Terms referring to the entire scleritome

The term *scleritome* (Bengtson 1985) is used to refer to the organizational plan of the entire assemblage for a given species. It is recommended that *sclerite assemblage* (Jell 1979) be used to refer to an actual set of associated sclerites recovered from the fossil record. They are together given preference over 'strobilus' (Pope 1975). The division of the scleritome into the longitudinal sectors 'head,' 'thorax,' and 'abdomen' (Dzik 1986) should be discontinued, as it carries organizational and phylogenetic connotations which are thus far unsupported. Likewise, the neutral term *sclerite* is preferred over 'elytrum' (Jell 1979; Dzik 1986).

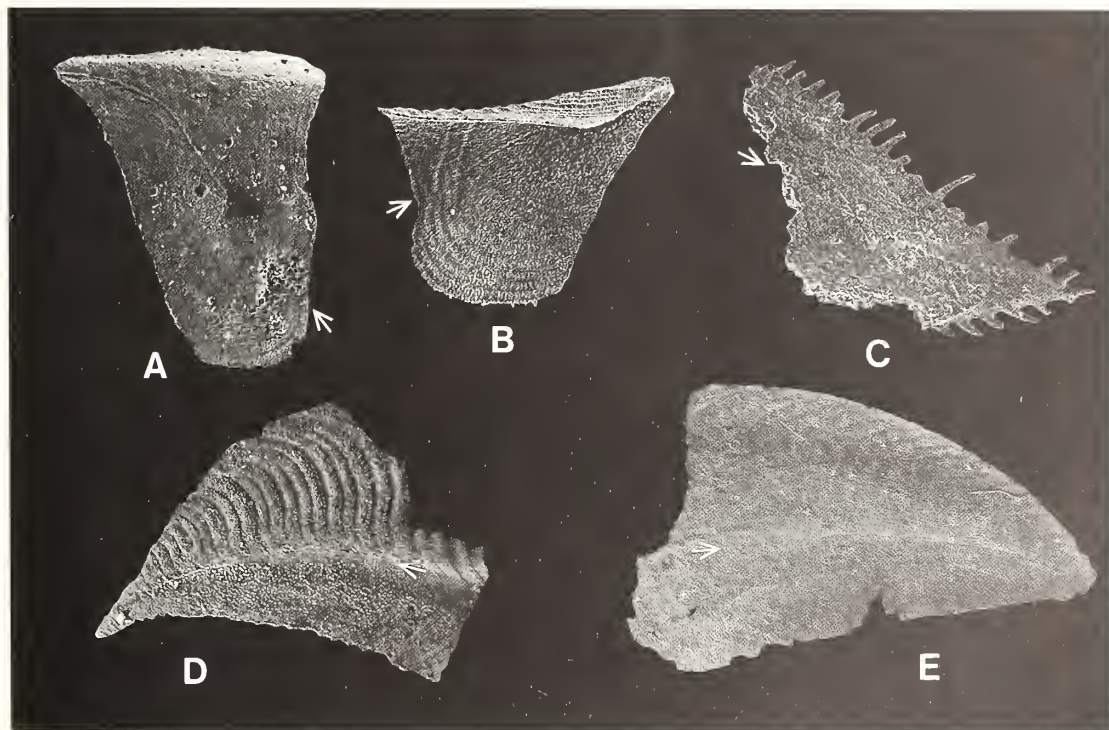
The longitudinal columns of a particular scleritome are referred to as *sclerite series*. Biserial machaeridians have left and right series. Quadriserial machaeridians have left and right *inner* and *outer* series. The rows of the scleritome may well correspond to particular body segments, if its fully segmented nature is indicative of true, and not merely functional, metamerism. It is not possible to evaluate this suggestion further, however, given our present state of knowledge of the group. Hence, the term 'segment' is used here in a phylogenetically neutral sense. When distinguishing between sclerites within a given series or set of series, reference should be made, where possible, to the sclerites of the *xth* segment, measured from the anterior of the scleritome.

Terms referring to individual sclerites

Bengtson (1978) has determined that machaeridian sclerites are composed of two distinct layers. An *outer layer* is composed of dense calcite, in which growth lines may often be visible (see Pl. 2, fig. 10),

and from which the rugae are formed (terms defined below). The *inner layer* is composed of distinct, densely packed lamellar elements which correspond closely to the granular texture of the inner sclerite surface. The layers may vary in thickness, depending upon the taxon in question. Bengtson (1978) noted that in the turrilepadid he investigated, two distinct layers did not appear to occur. In many silicified turrilepadid sclerites, the outer surface between the rugae has exactly the same granular texture as the inner surface. This indicates that the inner sclerite layer made up almost the entire sclerite thickness, with the outer layer confined to the rugae and not deposited between them.

Some of the following terms are illustrated in Text-figures 1–3. The *outer surface* of a sclerite is defined as that which bears the *rugae*. Rugae are prominent, ridge-like features, evenly spaced and developed parallel to the fine *growth lines*, apparently through deposition of additional material of the outer sclerite layer at specific growth increments. Rugae terminate before they reach the sclerite margin. Figured examples in which this appears not to be the case (e.g. Schallreuter 1985, pl. 2, figs 1–3) represent artefacts of poor preservation. Similar preservation has been observed by the authors in silicified material from the Canadian Arctic. Relatively coarse silicification often results in poorly preserved margins. The rugae seem to be more amenable to silicification in these conditions than the material of the margin and hence they are sometimes preserved while the margin lateral to them is not. They then protrude from the margin of the fossil sclerite, creating a false impression of having been extended into marginal spines in the living animal.

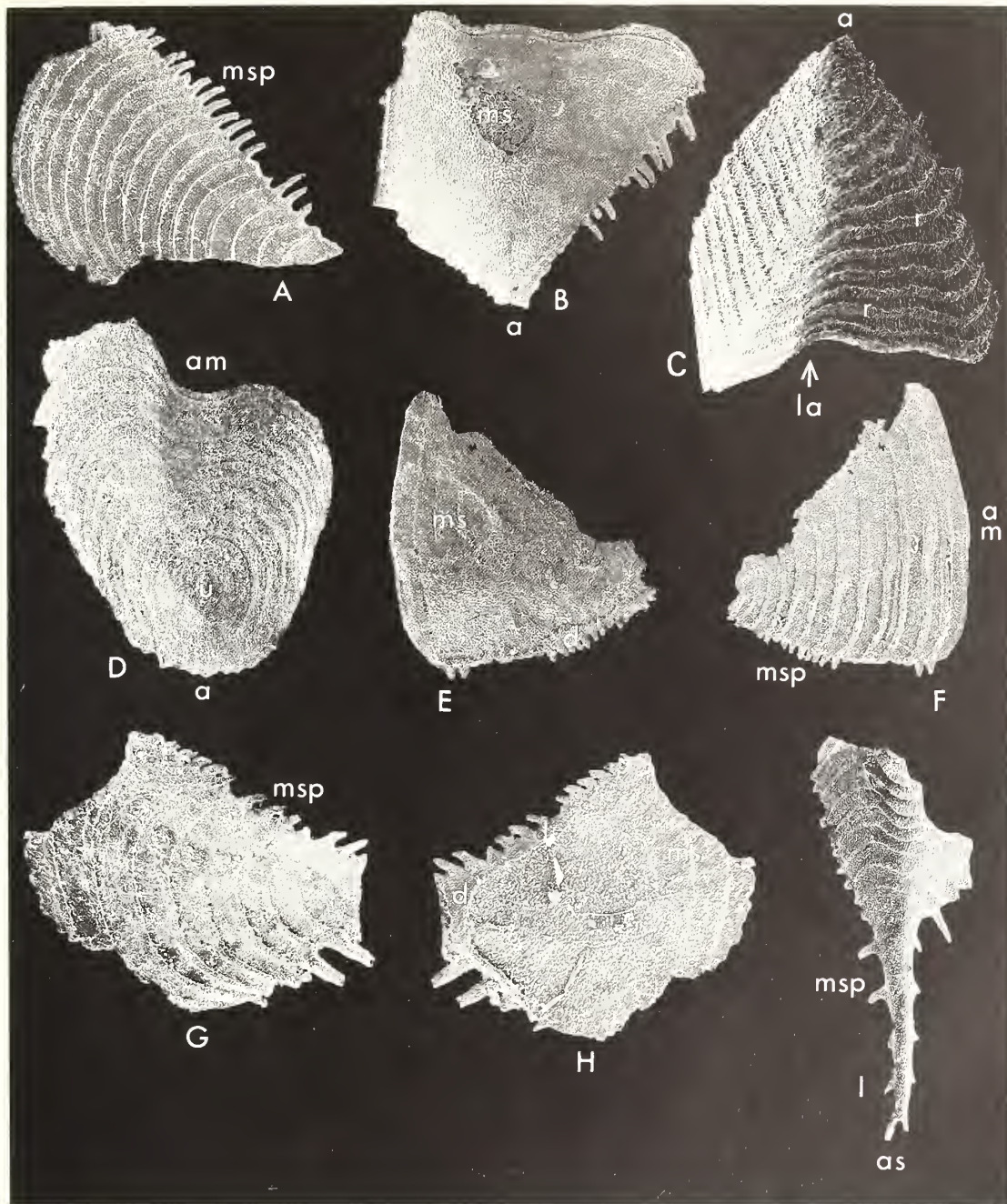


TEXT-FIG. 1. Silicified machaeridian sclerites from the Mackenzie Mountains, Northwest Territories, Canada, to illustrate the *inner groove* possessed by all machaeridian sclerites. The groove runs from the apex, and its anterior extent is indicated by an arrow in each case. All are scanning electron micrographs of the inner surface. A, UA 8125, left sclerite belonging to a new family of the Order Lepidocoleomorpha, AV 4 126, $\times 37$. B, UA 8126, right tongued lepidocoleid, AV 5 58–60, $\times 36$. C, UA 8127, outer right turrilepadid, AV 5 58–60, $\times 37$. D, UA 8128, outer right plumulitid, AV 4 126, $\times 18$. E, UA 8129, outer left plumulitid, AV 5 58–60, $\times 10$. See Over and Chatterton (1987) for locality information.

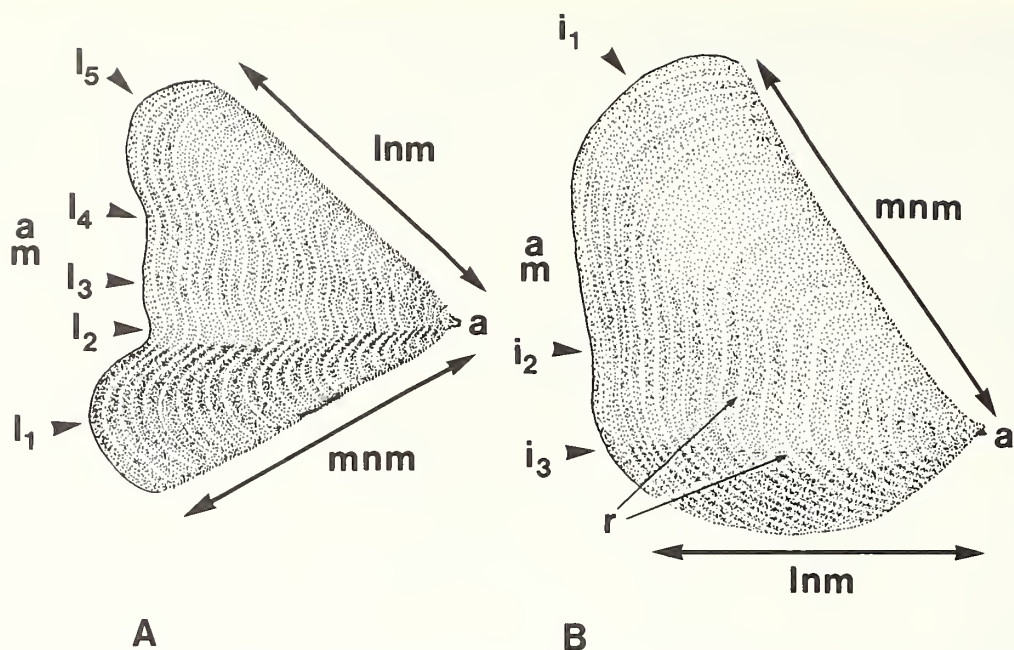
The *inner surface* has a finely granular texture, reflecting the regular arrangement of calcite elements in the inner sclerite layer. A single *muscle scar* is borne on the inner surface, although in some sclerites, particularly small ones and most Plumulitidae, it may be difficult to discern. A narrow groove runs anteriorly from the apex on the inner surface of all machaeridian sclerites (see Text-fig. 1). The function of this groove is not yet clear, but its universal occurrence suggests an intimate relationship with some fundamental aspect of machaeridian soft part anatomy. It is termed, for the time being, the *inner groove*. The *umbo* is the site of initial sclerite growth. It is usually located at the *apex*, but may sometimes be set somewhat forward, creating initially concentric growth lines (see Text-fig. 2D). The apex of turrilepadid sclerites is very often ornamented with a bifid *apical spine*, although this structure is frequently broken off before or after preservation. Some lepidocoleids also have an apical spine, but it seems never to have accessory spines developed upon it (see below), and invariably has a simple, not bifid, tip. All machaeridian sclerites have three margins (see Text-fig. 3). The *accreting margin* runs parallel to the growth lines and rugae, and is the front of deposition of new sclerite material. It may be further subdivided by folding of the sclerite in various types of machaeridians. The two *non-accreting margins* run from the apex to the edges of the accreting margin. The *medial margin* is that which lies closest to the dorsal midline of the assemblage, and its complement on the opposite side of the sclerite is the *lateral margin*. Many sclerites are folded about an angle which runs anteriorly from the apex to the accreting margin. This is the *longitudinal angle* (see Text-fig. 2C). When it occurs, it divides the accreting margin into *medial* and *lateral* parts. All known turrilepadids have *marginal spines* on the non-accreting margins. These spines are often continued on the lateral aspects of the apical spine, and are quite independent of the spacing of either the growth lines or the rugae, contrary to the claim of Dzik (1986, p. 119). In fact, the growth lines bend anteriorly near the sclerite margin, and in *Turrilepas modzalevskae*, can actually be seen to transect the marginal spines (see Pl. 2, fig. 10). This indicates that the marginal spines are formed from a different material to that which forms the outer surface. They seem either to have been formed from an accessory material deposited along the non-accreting margins as growth proceeded, or more likely from the material of the inner sclerite layer. Turrilepadid sclerites often have a distinct *doublure* (see Text-fig. 2B, E, H) preserved around the margins on the inner surface. The depositional and crystallographic characteristics of this feature are obscure, as it has thus far been observed only in well preserved silicified specimens. It is not clear whether or not it is a universal feature of turrilepadids. When it occurs, however, it is almost identical in texture to the marginal spines, and when viewing the inner surface, these spines seem to be lateral extensions of the doublural material. It seems likely, therefore, that the doublure is always present but often, like the marginal spines, not well expressed.

The pattern of rugae on the outer sclerite surfaces is constant within a sclerite type of a single species, and is therefore of much potential taxonomic value. To facilitate description and comparison, a system of numbering the inflections in the course of the rugae has been devised (see Text-fig. 3). This system is based upon sclerites of the genus *Turrilepas*, the best known turrilepadid. The general pattern and number of inflections seems on present evidence to be universal throughout Turrilepadidae, but this will require corroboration through further study. Numbering begins from the medial margin. Five inflections are present on inner sclerites, labelled I_1 – I_5 . The upper case 'I' is used for inner sclerites, and an 'R' or 'L' may be appended to distinguish between right or left sclerites. Outer sclerites feature only three inflections, labelled in lower case to distinguish them from inner sclerites, i_1 – i_3 . Thus, for example, I_1L refers to the first inflection of an inner left sclerite, while i_2R refers to the second inflection of an outer right sclerite. Note that although I_2 often coincides with the longitudinal angle of the inner sclerites (see, for example, Text-fig. 3A), this is not always the case, and the two terms refer to separate and distinct features.

Some combinations of features that may serve to characterize and distinguish between taxa include the degree to which each of the inflections is expressed, and the relationship between the longitudinal angle and the inflections. This system of numbering is adequate for reference to the Family Turrilepadidae. Some modification will be required for the plumulitids and lepidocoleomorphs, and will be presented elsewhere.



TEXT-FIG. 2. Silicified machaeridian sclerites from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada. All sclerites are from horizon AV 5 58-60, except I, which is from AV 2 248-8 (see Over and Chatterton 1987 for details). All are scanning electron micrographs. A-C and E-I are turrilepadids, D is a plumulitid. A, UA 8130, outer left sclerite, outer view, $\times 37$. B, UA 8131, inner right sclerite, inner view, $\times 36$. C, UA 8132, inner left sclerite, outer view, $\times 40$. D, UA 8133, inner right plumulitid sclerite, inner view (ridges are not rugae, but rather the impressions of the rugae borne on the outer surface), $\times 40$. E, F, UA 8134, outer right sclerite, inner and outer views, $\times 19$. G, H, UA 8135, outer left sclerite, outer and inner views, $\times 37$. I, UA 8136, inner right sclerite, outer view, $\times 20$. *a*, apex, *am*, accreting margin, *as*, apical spine, *d*, double lure, *la*, longitudinal angle, *ms*, muscle scar, *msp*, marginal spine, *u*, umbo.



TEXT-FIG. 3. Sclerites belonging to *Turrilepas wrightiana* (de Koninck), illustrating some of the terminology introduced. A, inner right sclerite. B, outer left sclerite. *a*, apex; *am*, accreting margin; *lnm*, lateral nonaccreting margin; *mnm*, medial nonaccreting margin; *l_x*, *x*th inflection of rugae, measured from medial margin, of inner sclerite; *i_x*, *x*th inflection of rugae, measured from medial margin, of outer sclerite; *r*, rugae.

SYSTEMATIC PALAEOLOGY

Class MACHAERIDIA Withers, 1926
 Order TURRILEPADOMORPHA Pilsbry, 1916
 Family TURRILEPADIDAE Clarke, 1896

Genera included. *Turrilepas* Woodward, 1865; *Deltacoleus* Withers, 1926; *Clarkeolepsis* Elias, 1958; *Spinacoleus* (= *Rugacoleus*) Schallreuter, 1985; *Mojczalepas* Dzik, 1986.

Diagnosis. Scleritome tightly articulated; sclerites usually large, thick, coarsely rugose; most sclerites with minute to robust bifid apical spine and multiple simple spines on non-accreting margins; mid-scleritome inner sclerites usually with longitudinal angle of about 90 degrees, sometimes more obtuse; medial area of inner left sclerites approximately twice that of inner right sclerites; rugae of inner sclerites usually with five inflections; rugae of outer sclerites with three inflections. For a given segment with four sclerites (i.e. any segment from 3 backwards), the outer sclerites overlap the inner sclerites on each side, and the medial portion of the inner right sclerite overlaps that of the inner left sclerite.

Remarks. It has not previously been appreciated that spinose non-accreting margins and apical spines are features which appear to occur in most turrilepadids. This is certainly because these features sometimes require extremely good preservation to remain evident. They are absent, for instance, from most of the *Turrilepas wrightiana* material from Dudley. Knowledge, however, of Canadian silicified material upon which detail is preserved to an exquisite degree, strongly indicates they are a constant feature. This is corroborated by the fact that in almost all of the Dudley

T. wrightiana specimens, the sclerite margins are either worn or broken off. Withers (1926, p. 41) did note the occurrence of marginal spines on some well-preserved specimens, particularly BM(NH) 59164. Reinvestigation of this specimen (see Pl. 1, figs 5, 7, 8) has shown that the spines are quite obvious. It must be emphasized that, contrary to occasional appearance (see for example BM(NH) 59406, Pl. 1, fig. 10), those Dudley specimens from which marginal spines appear to be absent have margins which have either been poorly preserved, have been broken prior to preservation, or most commonly have been broken and scored away during preparation in the nineteenth century. The apices of almost all of the sclerites collected from Dudley are missing. An exception is a mid-scleritome right inner sclerite on specimen BM(NH) 59406 (Pl. 1, fig. 10), which demonstrates unequivocally the presence of a minute, bifid apical spine.

Dzik (1986, fig. 4) has figured a poorly preserved sclerite from a Polish erratic boulder of Llanvirn age. He has made the following claims for this specimen: (1) that it is an outer plumulitid sclerite; and (2) that the marginal spines of the specimen coincide with the rugae. More material would be necessary to evaluate this taxon with any confidence, but the sclerite almost certainly represents a turrilepadid. Coincidence of the marginal spines and rugae cannot be properly evaluated on the basis of the published evidence, since Dzik did not figure the outer sclerite surface, upon which the rugae are borne. Faint ridges are evident on the inner surface, and these do appear broadly to match the marginal spines. It is possible that in particular sclerites the spacing of rugae may fortuitously approximate that of the marginal spines. The point that bears emphasis is that all other published illustrations of turrilepadid sclerites clearly indicate that there exists no general one-to-one relationship between the features, and their spacing, while it may occasionally match, is independent.

Genus TURRILEPAS Woodward, 1865

Type species. *Chiton wrightiana* de Koninck, 1857, from the Much Wenlock Limestone Formation of Dudley, West Midlands. By monotypy.

Other species. *T. modzalevskae* sp. nov.

Diagnosis. Turrilepadid machaeridians with minute apical spines; very small marginal spines, two or more occurring between each ruga; large, robust sclerites; twenty-five or more rugae on a single mature sclerite; I_1 – I_3 all well expressed; I_1 L sharp and angular, I_1 R broadly curving; i_1 – i_3 all well expressed, i_2 generally shallow; large, deep muscle scars on inner sclerites; scleritome subrectangular in mid-body cross section, with horizontal dorsal aspect and slightly ventromedially sloping lateral aspects.

Remarks. Only the type species and *T. modzalevskae* are assigned with certainty to this genus. Hall and Clarke (1888) erected eight new Devonian species, four of which were based upon single sclerites. This material requires re-examination before any taxonomic conclusions can be reached. *Turrilepas withersi* Elias and *T. japonicus* Kobayashi and Hamada both seem closer to *Deltacoleus*, discussed below. Both species, however, are at present too poorly known for use in comparative studies. Withers (1926) considered that material from Gotland figured by Aurivillius (1892) belonged to *T. wrightiana*. Bengtson (1979) listed the occurrence of *T. cf. wrightiana* and *T. n. sp.* from the Wenlock of Gotland, but the Gotland fauna remains to be investigated.

Turrilepas wrightiana (de Koninck, 1857)

Plate 1, figs 4, 5, 7, 8, 10–12; Plate 2, figs 6–9, 11–14

1857 *Chiton wrightianus* de Koninck, p. 199, pl. 1, fig. 2a–c.

1926 *Turrilepas wrightiana* (de Koninck); Withers, p. 37, pl. 5, figs 1–6; pl. 6, figs 1–8 (with full synonymy).

- ?1978 *Turrilepas* cf. *wrightiana* (de Koninck); Schrank, p. 10, pl. 1, fig. 3; pl. 2, figs 1 and 2; pl. 3, figs 1–3; pl. 4, fig. 1.
 ?1979 *Turrilepas* cf. *wrightiana* (de Koninck); Bengtson, p. 211.
 1986 *Turrilepas wrightiana* (Koninck); Dzik, p. 120, fig. 1B.

Holotype. BM(NH) I16283 (Pl. 1, Fig. 11).

Localities and distribution. Known from the Much Wenlock Limestone Formation, Dudley and Malvern; possibly occurs in the Wenlock of the island of Gotland, Sweden and an upper Wenlock erratic boulder from the island of Rügen, Baltic area, German Democratic Republic.

Diagnosis. A species of *Turrilepas* with at least twenty-six segments; marginal spines on medial non-accreting margins of inner sclerites spaced from two to four between each ruga; minute apical spines; length of accreting margin of outer sclerites subequal to length of longitudinal angle of outer sclerites.

Remarks. Schrank (1978) has figured some sclerites from an erratic boulder from the East German Baltic region, assigned to the upper Wenlock on the basis of the associated trilobite fauna, as *Turrilepas* cf. *wrightiana*. The sclerite illustrated in his plate 1, figure 3 does not belong to *Turrilepas*, but to another unnamed turrilepadid form, sclerites of which are known by the authors to occur in the Wenlock of northern Canada. The remainder certainly belong to *Turrilepas*. In number and spacing of marginal spines, the two inner sclerites figured by Schrank (1978, pl. 2, figs 1 and 2; pl. 3, fig. 1) resemble *T. wrightiana*, although the outer surface of a typical inner sclerite was not figured. The two outer sclerites, however, (Schrank 1978, pl. 3, figs 2 and 3) seem closer to *T. modzalevskae* in general shape. Further specimens would be required to determine the specific identity of this material.

Anterior structure. Withers (1926, p. 40) provided a discussion of the structure of the anterior end of the scleritome of *T. wrightiana*. His examples were specimens BM(NH) 59164 (Pl. 1, figs 5, 7, 8, 12) and BM(NH) 47871 (Pl. 2, figs 12–14), the anterior of which he exposed through careful preparation. At the anterior of both of these specimens there lies a small, almost flat sclerite with an odd orientation. This was interpreted by Withers as one of a pair of 'proximal' sclerites, the anteriormost sclerites that were supposed to function in attachment of the machaeridion to the substrate. We regard neither of these specimens as being true representations of the actual scleritome arrangement. BM(NH) 47871 has very obviously been disturbed, and although many of the modified anterior sclerites are present, the assemblage has been compacted, the

EXPLANATION OF PLATE I

Figs 1–3. *Deltacoleus crassus* Withers, 1926. Medial, dorsolateral, and lateral views of holotype BM(NH) In23708, inner right sclerite, Balclatchie Group, Balclatchie, Upper Ordovician, $\times 9$.

Figs 4, 5, 7, 8, 10–12. *Turrilepas wrightiana* (de Koninck, 1857). 4, BM(NH) I16308, left outer sclerite, view of outer surface, Wenlock Limestone, Malvern, Middle Silurian, $\times 5$. 5, 7, 8, 12, BM(NH) 59164, nearly complete assemblage, Wenlock Limestone, Dudley, middle Silurian; 5, entire specimen, dorsolateral view, $\times 2.5$; 7, detail from mid-body, dorsal view, note marginal spines, $\times 5$; 8, detail from anterior of assemblage, dorsolateral view, note marginal spines, $\times 6$; 12, detail of anterior end of assemblage, note loss of outer right series and truncation of anterior end of assemblage, $\times 4$. 10, BM(NH) 59406, Wenlock Limestone, Dudley, Middle Silurian, detail from midbody of articulated assemblage, right lateral view, note apical spines, $\times 4$. 11, BM(NH) I16283, holotype, Wenlock Limestone, Dudley, Middle Silurian, right inner and left inner sclerites, Wenlock Limestone, Dudley, Middle Silurian, $\times 3.5$.

Fig. 6. External mould, BM(NH) In23673, assigned to *Deltacoleus crassus* by Withers (1926), but of indeterminate affinities. Inner left sclerite, Balclatchie Group, Dow Hill, Upper Ordovician, $\times 4$.

Fig. 9. BM(NH) In23737, assigned to *Deltacoleus crassus* by Withers (1926), in fact a plumulitid. Outer right sclerite, internal mould with sclerite fragment, view of outer surface, Stinchar Limestone, Aldons, Middle Ordovician, $\times 4$.



relationships between sclerites distorted, and some sclerites lost. BM(NH) 59164 is likewise partially complete, but is missing almost all of its anteriormost sclerites, in addition to the complete right outer series for the anterior half of the sclerite assemblage.

A specimen that provides what appears to be an accurate idea of the anterior structure is known, however. This is BM(NH) I16282 (Pl. 2, figs 6–9, 11), a specimen mentioned but not figured by Withers (1926, p. 38). The outer left series is concealed by the matrix in this example, but all other anterior sclerites seem to be present. The structure of the specimen is described below.

Inner right series sclerites of segments 1–7 are present. Outer right series sclerites of segments 3–6 are present, but some are fractured and fragmentary. Inner left series sclerites 1–5 are present, and an inner left sclerite of an indeterminate more posteriorly placed segment is also evident, displaying a relatively long, bifid apical spine (see especially Pl. 2, fig. 9). Anteriorly in the sclerite series, the inner right sclerites tend to flatten out, and the sclerite of segment 1 all but lacks a longitudinal angle. Conversely, the inner left sclerites become increasingly folded, the longitudinal angle becoming acute. The inner left sclerites of segments 2 and 3 are intact on the specimen. The sclerite of segment 1 has been broken just beneath its longitudinal angle (see Pl. 2, fig. 11), and the lateral portion has folded inward, giving the longitudinal angle a slightly more acute appearance than is in fact the case. The outer right sclerites begin with segment 3, and except for a slight increase in the length of the accreting margin posteriorly in the series, the initial segment is of very similar form to successive ones in the series.

The sclerites of segment 1 are distinctive. The right sclerite has a very wide accreting margin relative to the length of the longitudinal angle. Both sclerites have extremely closely spaced rugae. The inner sclerites of segment 2 are intermediate in morphology between those of segments 1 and 3. By segment three, the sclerites have attained the general form of successive sclerites in their respective series, and the major changes thereafter are restricted to the longitudinal angles moving towards a stable value of approximately 90 degrees.

As regards Withers's example, BM(NH) 47871, the 'proximal plate' with the anteriorly directed apex at the anterior of the assemblage (Pl. 2, fig. 12) is almost certainly the inner left sclerite of one of the anterior segments, possibly 2 or 3, with most of its lateral portion broken off just beneath the longitudinal angle (compare with the fractured segment 1 sclerite in Pl. 2, fig. 11). The sclerites of segment 1 have been lost, and the broken inner left sclerite has been displaced to overlie the accreting margin of the inner right sclerite of segment 2. The inner left sclerite of this segment is intact and in proper spatial relation to its right side counterpart. All of these sclerites, however, have been compacted and slid backward on the truncated assemblage, so that they sit atop an inner right sclerite (see Pl. 2, fig. 13), probably of segment 4.

Comparison of Plate 2, figure 6 with Jell's (1979) figure 4D reveals an essential similarity in structure between the segment 1 sclerites of turrilepadids and those of plumulitids. The sclerites are all but identical in shape and the course of the rugae. Furthermore, both families lack outer series sclerites on the first two segments. Jell's (1979) material established this fact for plumulitids, while the present material provides strong evidence for this condition in turrilepadids.

Accretionary growth. It is notable that within a given sclerite assemblage, all sclerites appear to bear approximately the same number of rugae. On specimen BM(NH) I16282, described above, for instance, the inner left sclerite of segment 1 has twenty-seven discernible rugae. The inner right sclerites of segments 1 and 2, both of which are incomplete, have nineteen and eighteen rugae respectively. The inner left sclerite of segment 4 has twenty-five rugae, as does the inner right sclerite of segment 5. The outer right sclerite of segment 5 is incomplete, but has twenty-four discernible rugae. The rugae are very closely spaced on sclerites of the first

EXPLANATION OF PLATE 2

Figs 1–5, 10. *Turrilepas modzalevskae* sp. nov. BM(NH) In63310, Lower Ludlow, Konovka Formation, Podolia, Ukraine, USSR, holotype. 1, dorsal view. 2, right lateral view. 3, left lateral view. 4, posterior view. 5, anterior view. All $\times 4$. 10, detail of medial aspects of inner sclerites, note rugae, growth lines, marginal spines, and manner in which growth lines transect marginal spines, $\times 14$.

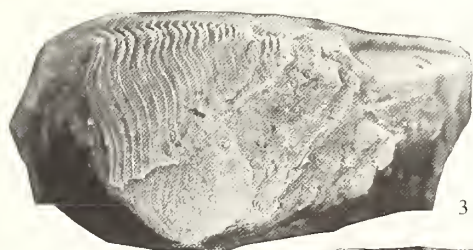
Figs 6–9, 11–14. *Turrilepas wrightiana* (de Koninck). 6–9, 11, BM(NH) I16282, the anterior end of an assemblage, Wenlock Limestone, Dudley, Middle Silurian; 6, detail of anteriormost sclerites, $\times 4.5$; 7, dorsolateral view of medial aspects of inner sclerites, $\times 2.5$; 8, dorsal view, $\times 2$; 9, right lateral view, $\times 2.5$. 11, view of lateral aspects of inner left sclerites, $\times 4.5$. 12–14, BM(NH) 47871, a disturbed anterior end of an assemblage, Wenlock Limestone, Dudley, Middle Silurian; 12, the anteriormost sclerites, exposed by Withers, see text for explanation, $\times 8$; 13, dorsal view, $\times 2.5$; 14, left lateral view, $\times 2.5$.



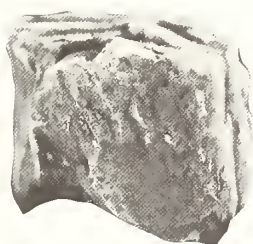
1



2



3



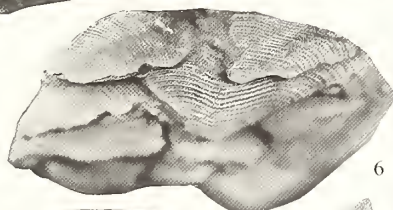
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5



7



6



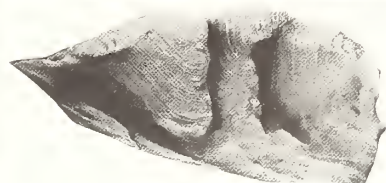
8



9



10



11



12



13



14

series, and there seems to be a fairly constant relationship between the size of the sclerite and spacing of the rugae. All of this indicates that the scleritome very likely had a fixed number of segments, and that growth was incremental, with rugae deposited one at a time, at the same time for all sclerites in the assemblage. The pattern observed is incompatible with serial addition of segments. This information, if it can be corroborated through further study, has important implications for reconstruction of machaeridian scleritomes when only disarticulated sclerites are available, the general case in the palaeontological record. If this relationship holds true, it can effectively be assumed that conspecific sclerites with a roughly equivalent number of rugae can be accommodated together in the same scleritome reconstruction.

Turrilepas modzalevskae sp. nov.

Plate 2, figs 1–5, 10

Etymology. For Dr T. L. Modzalevskaya.

Holotype. BM(NH) In63310, a unique specimen from the Konovka Formation (lower Ludlow), Podolia (for detailed locality see above), comprising parts of four segments from the mid-body of an articulated sclerite assemblage.

Diagnosis. A species of *Turrilepas* with extremely small, closely set marginal spines, five to seven between rugae of inner sclerites; I_1 crisply defined, about 100 degrees; at least twenty-eight rugae on mature sclerite; accreting margin of outer sclerites about two-thirds to three-quarters length of longitudinal angle.

Remarks. *Turrilepas modzalevskae* may be distinguished from *T. wrightiana* by a greater number of smaller, more closely spaced marginal spines, rugae which tend to run straighter between inflections, making the inflections slightly sharper, and especially by outer sclerites with accreting margins that are much shorter relative to the length of the longitudinal angle, giving the sclerites a less erect, more anteroposteriorly elongate appearance.

The specimen consists of an articulated portion of a sclerite assemblage, probably from some point along the undifferentiated midbody area. Very little displacement has occurred among those sclerites present, and the spatial relationships between sclerites appear to reflect those prevalent during the life of the animal. The specimen comprises two nearly complete and three partially complete inner right sclerites (the posteriormost having slipped medially to lie behind the sclerites of the inner left series), three nearly complete outer right sclerites, one nearly complete and two partially complete inner left sclerites, and one partially complete outer left sclerite.

Genus DELTACOLEUS Withers, 1926

Type species. *Deltacoleus crassus* Withers, 1926, from the Caradoc of the Balclatchie Group, Girvan, Ayrshire.

Other species. None.

Remarks. Withers (1926) established *Deltacoleus* as a monotypic genus, based upon only five disarticulated sclerites. Two were inner sclerites from the Upper Ordovician (Caradoc) of Balclatchie, one of which he selected as the holotype. Three were outer sclerites from the Middle Ordovician (Llandeilo) of Aldons. The holotype (Pl. 1, figs 1–3) is reasonably well preserved, but is missing most of its left non-accreting margin. It is an inner right sclerite, and has a distinctive morphology as follows: medial area about three-quarters the size of lateral area, compared with about one-half in *Turrilepas*; longitudinal axis gently curving, compared with essentially straight in *Turrilepas*; I_1 R quite angular, not as broadly curving as in *Turrilepas*; I_2 R very shallow, occurring on medial area, while deep and placed at or lateral to the longitudinal angle in *Turrilepas*; I_3 R occurring on longitudinal angle; I_4 R and I_5 R spaced respectively about one-third and two-thirds of

the way between longitudinal angle and medial non-accreting margin, both shallow; at least thirty-six rugae; apical portion of sclerite slightly beaked.

The second inner sclerite, from the inner left series, is represented by internal and external moulds (the external mould figured in Plate 1, figure 6, the internal figured by Withers 1926, plate 6). While it shares a curving longitudinal axis with the first sclerite, it is otherwise much larger and of quite different appearance, with I_1L placed very near to the longitudinal angle, and I_2L – I_5L all occurring on the lateral aspect of the sclerite, as in *Turrilepas*. This sclerite is almost certainly not conspecific, and probably not even congeneric, with the holotype.

The outer sclerites are from much older rocks. The example figured by Withers (1926, pl. 8, fig. 8) is an internal mould with a fragment of sclerite material preserved of a left outer plumulitid sclerite. Withers (1926, p. 44) declined to refer it to the plumulitids because the specimen lacked a longitudinal fold, a feature he considered diagnostic. As is evident from the rephotographed specimen (Pl. 1, fig. 9), a weak dorsal inflection is present, consisting of two 'longitudinal folds', one at the midpoint between the non-accreting margins and one placed near the medial non-accreting margin, with the thickness of the sclerite inflected slightly dorsally between them. Comparison of the sclerite with the as yet undescribed silicified sclerite of Text-figure 1E confirms that it belongs within the Plumulitidae.

Hence, *Deltacoleus* appears to have been erected as something of an odds-and-ends taxon. Clearly, the concept of the genus must be based solely upon Withers's holotype. This is an unsatisfactory basis for comparison and more material would be required from the type area to properly delineate the taxon. The sclerites figured by Schallreuter (1985, pl. 1, figs 2–5) as *Deltacoleus erraticus* and *Deltacoleus? crenulatus* bear little resemblance to the holotype, and should be excluded from the genus. Schallreuter's (1985, pl. 1, fig. 1) *D. cf. crassus* is very similar to the holotype. This single sclerite certainly belongs to *Deltacoleus*. Whether or not it is conspecific with *D. crassus* can only be determined through further collecting of both the Scottish and German material. Dzik (1986, fig. 7) has figured three specimens from the Llanvirn and Arenig of Poland as *Deltacoleus cf. crassus*. The Llanvirn specimens (Dzik 1986, fig. 7A,B) seem conspecific (they are from the same erratic boulder), and may belong to *Deltacoleus*, although likely not to *D. crassus*. The affinities of the Arenig fragment (Dzik 1986, fig. 7C,D) are indeterminate.

In sum, before this genus can be of any use in comparative phylogenetic studies, thorough redescription of all its possible members will be required.

Genus CLARKEOLEPIS Elias, 1958

Type species. Designated herein as *Clarkeolepis clarkei* Elias, 1958, from the Mississippian Redoak Hollow Formation of Oklahoma.

Remarks. Elias (1958) described three machaeridian species, *Turrilepas whithersi* (discussed above), *Clarkeolepis clarkei*, and *C. elegans*. As he did not name a type species for the genus, *C. clarkei* is selected herein by virtual tautonymy and pagination. *C. clarkei* is known from two figured sclerites, and *C. elegans* from one. All three are likely conspecific, and hence *C. elegans* should likely be considered a subjective junior synonym of *C. clarkei*.

The sclerites assigned to *Clarkeolepis* are certainly machaeridians, but are characterized by a very low number of rugae (about ten), and an odd raised ornament apparently transecting the spaces between the rugae. More material and more thorough treatment is needed before any taxonomic conclusions, save to assert that the sclerites seem to belong in the Turrilepadidae, can be reached.

Genus SPINACOLEUS Schallreuter, 1985

Nomenclatural note. Schallreuter (1985) used the genus name *Spinacoleus* in his text, but *Rugacoleus* in the explanation of his figures. Article 24(b) of the ICZN requires that the first reviser cites the alternative names

together and chooses one as the correct name. Dzik's (1986) listing of *Spinacoleus* did not fulfil this requirement and is therefore not binding. In the interests of nomenclatural stability, however, *Spinacoleus* is selected here as the valid name.

Type and only species. *Spinacoleus breugmanni* Schallreuter, 1985, from Öjlemyrflint erratic boulder No. G16.

Remarks. The holotype and paratype material (Schallreuter 1985, pl. 2, figs 1–3) is poorly preserved. As mentioned above, the sclerite margins are missing from this material, giving the false impression that the rugae are extended into marginal spines. A more accurate impression is given by the better preserved sclerites questionably assigned to the species by Schallreuter (1985, pl. 2, figs 4, 6, 7), in which the rugae clearly terminate short of the sclerite margin, and the marginal spines are distinct and not spaced in any set relation to the rugae.

Schallreuter's (1985) material is without question properly associated and belongs to a distinctive turrilepadid form. Although it remains inadequately known, *Spinacoleus breugmanni* is sufficiently well described to allow comparison with other machaeridians. Hence, further work on machaeridian taxonomy may lead to a better understanding of this genus.

Genus MOJCZALEPAS Dzik, 1986

Type and only species. *Mojczalepas multilamellosa* Dzik, 1986, from Llanvirn strata (*E. reclinatus* Zone), Mójca Limestone, Holy Cross Mountains, Poland.

Remarks. Dzik (1986, fig. 5) figured only two fragmentary and poorly preserved inner sclerites when he erected this taxon. Unfortunately, these sclerites give no satisfactory idea of the structure, shape, or pattern of rugae of the originals. As such, there does not seem to exist an objective basis for reference of further material to this taxon or for comparison with other turrilepadid forms. Satisfactory incorporation of this taxon into a general scheme of machaeridian classification must await adequate redescription and illustration.

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MOSASAURS FROM THE UPPER CRETACEOUS OF NIGER

by T. LINGHAM-SOLIAR

ABSTRACT. Fragmentary remains from the Dukamaje Formation ('*Mosasaurus* Shales'), Upper Maastrichtian, S.W. Niger, reveal a diverse mosasaur fauna of at least six genera – *Goronyosaurus*, *Igdamanosaurus* nov. gen., *Angolasaurus*, *Halisaurus*, *Plioplatecarpus*, *Mosasaurus*, and possibly *Platecarpus*. This represents an astonishingly high number of mosasaur genera from a single horizon, equalling that of the most prolific mosasaur beds of the world, the Niobrara Formation of Kansas, U.S.A. and the Craie Phosphatée de Ciply, Belgium. *Plioplatecarpus* represents the first documentation in Africa of this genus.

MOSASAURS were large marine lepidosaurian reptiles which, in a brief 25 million years, dominated the Late Cretaceous seas. Remains are found on all continents including Antarctica (Chatterjee *et al.* 1984). On the basis of skull form and, to a lesser extent, postcranial characters, they have been divided into three subfamilies, the Mosasaurinae, Tylosaurinae, and Plioplatecarpinae. Russell (1967) established, in addition, several tribal categories, for example, the Mosasaurini and Globidentini.

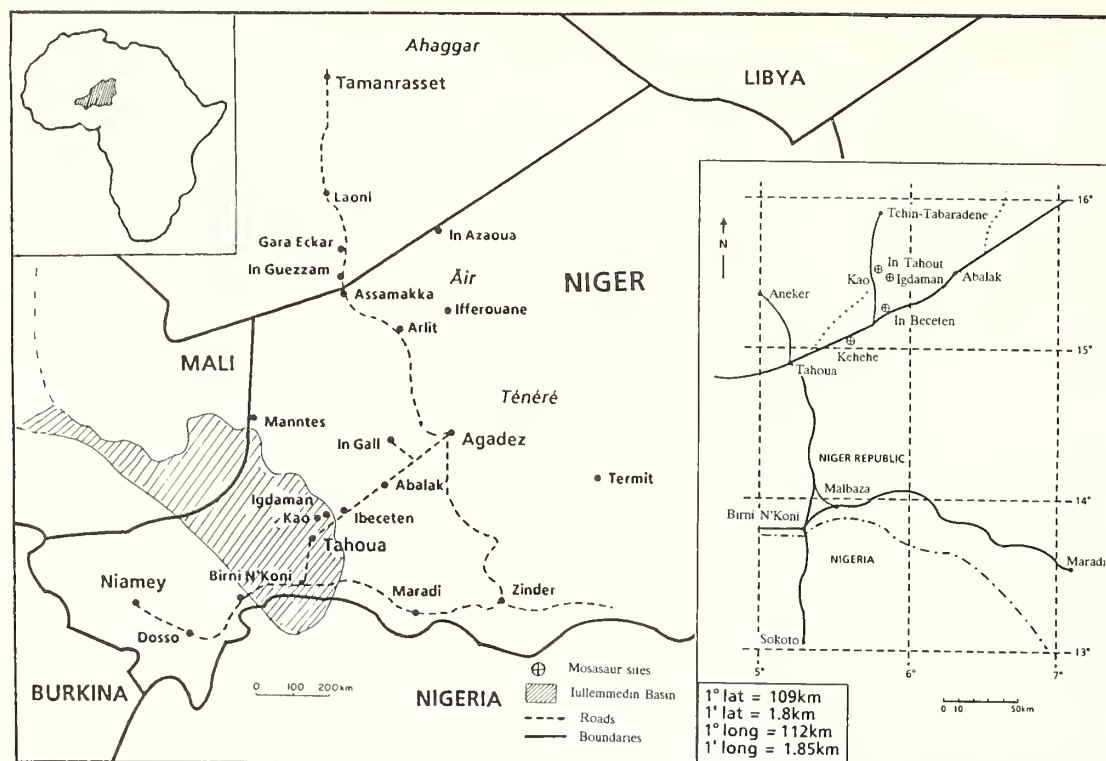
The majority of mosasaur remains occur in North America, in particular the Niobrara Chalk of Kansas, and the Gulf Coast, the Phosphatic Chalk of Ciply, Belgium, and the Tuffeau of Maastricht, the Netherlands (Russell 1967, charts 4, 5; Lingham-Soliar and Nolf 1989). Most other areas of the world have yielded isolated finds. However, two further areas, in Africa, are noteworthy, with perhaps the best mosasaur material known outside the North American and European sites: the '*Mosasaurus* Shales' (Upper Maastrichtian, Dukamaje Formation) of Sokoto State, N.W. Nigeria (Swinton 1930; Azzaroli *et al.* 1972, 1975; Halstead 1979; Soliar 1988) and the grey limestone coastal cliffs (Upper Turonian, 'Camadas do Tadi') of Iembe, Angola (Antunes 1964; Lingham-Soliar, in prep.).

In 1988 a joint expedition to Niger by the British Museum (Natural History), London, and Kingston Polytechnic recovered mosasaur remains, which Cyril Walker of the BMNH, the leader of the expedition, and responsible for collecting some significant specimens, placed at my disposal. The material, although fragmentary, was the first record of reptiles from the Maastrichtian of Niger. The only previous documentation of vertebrates from this horizon is of fishes (Tabaste, 1963; Capetta 1972).

Repository abbreviations are: BMNH, British Museum (Natural History); GSN Geological Society of Nigeria; IRSNB, Institut Royal des Sciences Naturelles de Belgique; IGF, Institute of Geology and Palaeontology of the University of Florence; YPM, Yale Peabody Museum. All the material described, unless otherwise stated, is housed in the BMNH.

GEOLOGY

The following outline of the geology of Niger is my interpretation of information from David Ward and Richard Moody. The three principal localities, In Tahout, Mt Igdaman, and Kehehe, lie in the south-western corner of Niger, in an area bordering Dahomey in the south west, Nigeria in the south and Mali in the west (Text-fig. 1). This region was once part of the large West African intracontinental sedimentary basin, the Iullemmeden Basin. According to Petters (1977, 1979a), the subsidence of the South Central Saharan platform during Maastrichtian times created a marine embayment of the Tethys sea with its southern limits in the south-



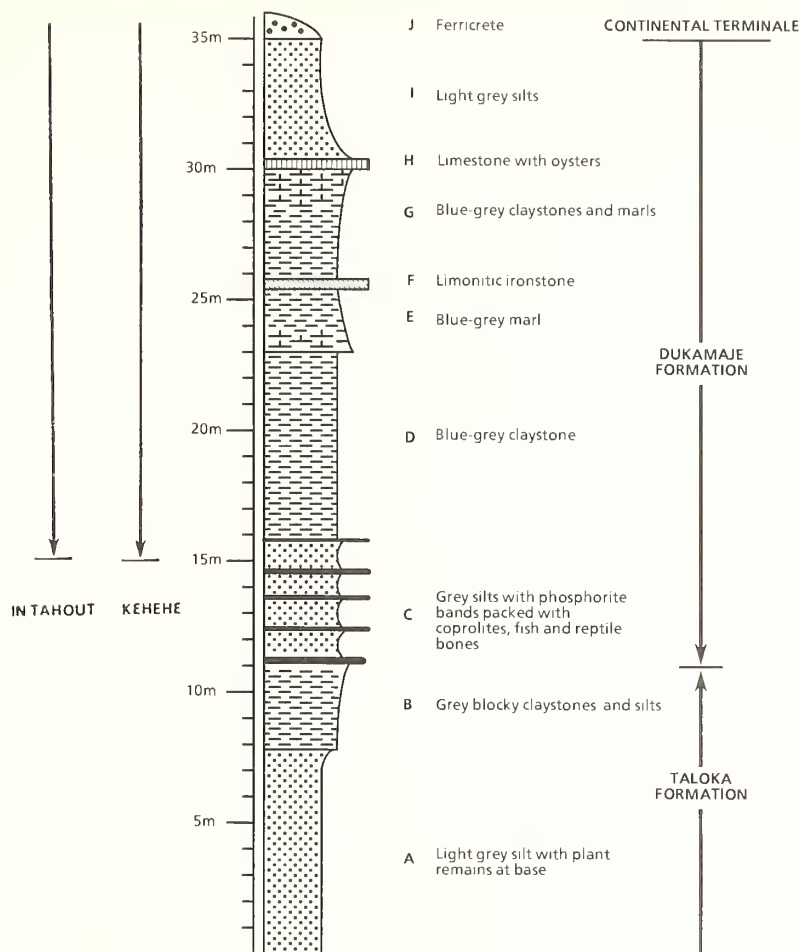
TEXT-FIG. 1 Map of Niger showing location of Igdaman, In Tahout and Kehehe (right inset, detail; David Ward pers. comm.). The Iullemmeden Basin (shaded) is figured after Petters (1977).

western part of Niger Republic and extending into the north-western tip of Nigeria. Other authors (Reyment 1965; Kogbe 1973; Adeleye 1975; Howarth 1981), in contrast, take the view that the trans-Saharan seaway was open-ended, joining the Mediterranean with the Gulf of Guinea.

The Maastrichtian horizon of N.W. Nigeria has been described in detail (reviewed Soliar 1988). Kogbe (1979) reported that '... similar fossil beds also occur in Niger Republic ...' where they '... outcrop extensively'. However, there is no record, to my knowledge, of detailed stratigraphical work on this horizon in Niger besides brief mention by Greigert (1966) and Krasheninnikov and Trofimov (1969). The three localities represent exposures of the Late Cretaceous (Maastrichtian) Dukamaje Formation (David Ward, Richard Moody, pers. comm.). A detailed stratigraphic section is available for Igdaman and tentative results for the other two areas (Text-fig. 2).

In Tahout ($5^{\circ} 52' 15'' 22'$), near Kao, a previously unrecorded locality, shows exposures of a complete series of sections of the Dukamaje Formation, with the mosasaurs coming from the lower levels on or very near the Cretaceous/Tertiary boundary. Above this lie the Palaeocene phosphate beds. Kehehe ($5^{\circ} 36' 15'' 2'$) represents an outcrop of Late Cretaceous 'Mosasaurus Shales', the beds resembling those described at Gilbedi and Kaffe (Reyment 1965). Of the three localities, Mt Igdaman ($5^{\circ} 50' 15'' 23'$; Greigert 1966) yielded the largest amount of mosasaur material. Earlier work by Cappetta (1972) has shown the horizon to be abundant in inshore and marine fish remains which were apparently collected from a single thick phosphatic bed (David Ward, pers. comm.). Outcropping all the way around the hill are a series of bone beds from which the reptile and fish remains were obtained. This 'Mosasaurus Shales', or Dukamaje Formation, is both overlain and underlain by loose sandstones equivalent to the Nigerian Wurno and Taloka Formations respectively (Text-fig. 2).

In addition to mosasaur material, the above horizons yielded the remains of a number of vertebrates, some similar to those found in the 'Mosasaurus Shales' of Nigeria: the sea snake *Palaeophis*, pelomedusid turtles, sharks (including sawfish sharks and rays), cat fish, and the remains of the marine teleost, *Stratodus* (David Ward, pers. comm.).



TEXT-FIG. 2 Stratigraphic section at Igdaman (David Ward pers. comm.) with approximate extent of sections at In Tahout and Kehehe.

SYSTEMATIC PALAEOONTOLOGY

Order SQUAMATA

Family MOSASAURIDAE

Subfamily *Incertae Sedis*

Genus *Goronyosaurus* Azzaroli *et al.*, 1972

Goronyosaurus sp.

Text-figures 3, 4

Referred material. Premaxilla and two fragments of maxilla (R11909), probably associated. Poorly preserved dentary (R11947) with tooth sockets and remains of teeth, probably from a different individual. Mt Igdaman.

Revised diagnosis. Premaxilla lacking rostrum extends on to wide internarial bar; closed canal for olfactory lobes; ectopterygoid processes dorsoventrally flattened, two fork-like processes; snout approximately 55% total length of skull; maxillary teeth no more than 11, extend close to posterior

border of the orbit; deep lateral interdental pits; little tapering of the dentary anteriorly; very high number of large foramina on premaxilla; elongated anterior tooth bases.

Description. A series of unique interdental pits on the jaw rami of specimens R11909 and R11947, and on the dental rami of the holotype of *G. nigeriensis* (IGF 14750, Azzaroli *et al.* 1975; Soliar 1988) characterise the genus *Goronyosaurus*.

Premaxilla. The premaxilla R11909 (Text-fig. 3A, B) is broken at a point just anterior to its union with the maxilla. No teeth are present, only four large sockets. The most striking condition of the premaxilla is the presence of a large deep interdental pit located laterally between the first and second premaxillary teeth (Text-fig. 3B). The premaxilla also shows an unusually high number of large foramina for the exits of cranial nerve V (ophthalmic branch), approximately 15 on either side, situated on the lateral and anterodorsal surfaces and extending close to the midline. The premaxilla is blunt, similar to that of *Prognathodon* (Russell 1967; Lingham-Soliar and Nolf 1989).

Despite poor surface preservation, the right premaxilla of *G. nigeriensis* (IGF 14750) shows approximately 10 foramina in a small area. In other mosasaurs, the number of large foramina generally does not exceed 6–7 on either side. In tylosaurs such as *Tylosaurus* (*Liodon*) *dyspelor* (Cope 1875, pl. 28), there are few large foramina, the majority being small, situated in a cluster on the lower lateral and ventral surface of the premaxilla.

Maxilla. Two well preserved fragments of maxilla, probably part of the same specimen R11909 (Text-fig. 3C, D), reveal the characteristic deep interdental pitting. Tooth crowns are not preserved, only an unusually long and well preserved tooth base (Text-fig. 3D) reminiscent of the one noted in the maxilla of the holotype of *Goronyosaurus* (Soliar 1988, fig. 3A; Text-fig. 10A). There are no more than eleven maxillary teeth in IGF 14750 although arguably there may be as few as nine if the two teeth at the end of the ramus are in fact displaced posterior pterygoid teeth (Text-fig. 10A).

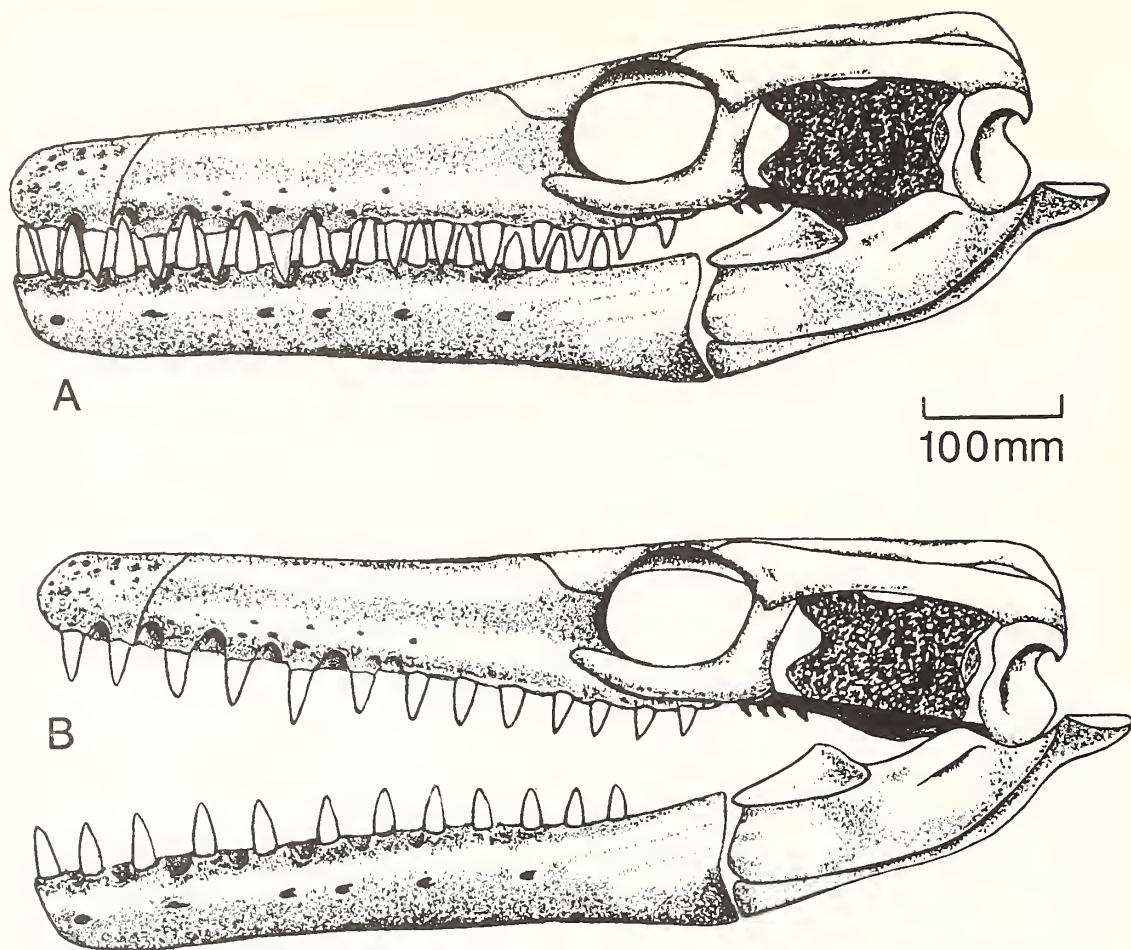
Dentary. The left dentary (R11947) is complete, although fractured into four separate fragments (Text-fig. 3E, G), and represents the first complete dentary of *Goronyosaurus* to be reported. It is fairly slender and scarcely tapers anteriorly, contrasting with the usual description of the element in mosasaurs: '... an anteriorly narrowing girder of bone...' (Russell 1967, p. 49). Medially, the excavation for Meckel's cartilage extends up to the second dentary tooth. All that remains of the teeth are six tooth bases and six poorly preserved relatively straight tooth crowns (Text-fig. 3E, G). The strongest indication that the dentary is referable to *Goronyosaurus* lies in the deep lateral interdental pits, extending to about the seventh tooth (Text-fig. 3G), which accords closely with those of the maxilla and the condition seen in the holotype material. Marginal teeth of R11909, R11947, and of the holotype are widely spaced.

Discussion. In occlusion, the jaws fitted tightly together, with the teeth overlapping their opposite numbers and fitting, uniquely for mosasaurs, into the deep interdental excavations (Text-fig. 4A). *Plotosaurus* (Camp 1942, pl. 1) shows a form of dental interdigitation, although there are no excavations for the opposing dentition – the battery of teeth (the highest number found in mosasaurs, 18 on the maxilla and 17 on the dentary) presumably formed a fish trap resembling that seen in plesiosaurs (McFarland *et al.* 1979; Brown 1981). In certain smaller specimens of *Mosasaurus hoffmanni* (e.g. IRSNB 1559, 'R12') a form of shallow interdental pitting is observed, but it is scarcely comparable with that of *Goronyosaurus*. However, Marsh (1869, p. 394) described 'the unusual depth of pits' on the outer superior edge of the lower jaw of *Mosasaurus copeanus* (synonymised *Plioplatecarpus depressus*; Russell 1967), the only record of this character in the literature, to my knowledge. Further study of this material is essential as it is probable that it belongs to a form related to *Goronyosaurus*.

The long snout of *Goronyosaurus* indicates that the adductor muscles originated relatively far back on the robust temporal arcade (Text-figs 4, 10). It is probable that static or bite forces were consequently reduced (Olson 1961; Greaves 1983), but that speed of jaw closure was conversely increased. A similar form of 'snapping' jaw mechanism was apparently prevalent in long-snouted marine crocodiles such as the Palaeocene *Rhabdognathus* and *Dyrosaurus* of the Sokoto area in N.W. Nigeria (Buffetaut 1976, 1979, p. 35). This technique of rapid impaling of prey was



TEXT-FIG. 3. *Goronyosaurus* (A-E, R11909). A, B, dorsal and lateral views of premaxilla. C, D, maxilla fragments. E, ventral view of C. $\times 1$. F, G, R11947, medial and lateral views of left dentary. $\times 0.5$.



TEXT-FIG. 4. Reconstruction of the skull of *Goronyosaurus nigeriensis* based on specimens IGF 14750, BMNH R11909, and R11947. A, jaws in occlusion, B, jaws open. $\times 0.2$.

undoubtedly effective in capturing fairly evasive, moderately small, reptiles and fishes. The long pointed, relatively straight teeth in the dentary (R11903), long tooth base in the maxilla (R11909) and in the holotype (Soliar 1988; Text-fig. 10A), are consistent with such an hypothesis (Text-fig. 4).

The condition of interdental pits in *Goronyosaurus*, first figured in the holotype (Soliar 1988, fig. 3), represents an autapomorphy of the genus. The condition has also enabled a re-evaluation of previously mis-identified mosasaur material. For instance, the dentary of '*G.*' *nigeriensis*, figured by Azzaroli *et al.* (1975, pl. 1a, b), lacks interdental pits, suggesting that it is not referable to the genus, whereas a previously undescribed fragment of dentary (IGF 14751/2), revealing a series of deep external interdental pits, clearly is. Furthermore, two highly gypsiferous dentary fragments (R5682, R5683) referred to *Mosasaurus nigeriensis* (Swinton 1930), demonstrate the characteristic interdental pits of *Goronyosaurus*.

Subfamily ?PLIOPLATECARPINAЕ

Igdamanosaurus gen. nov.Type species *Igdamanosaurus aegyptiacus* Zdansky, 1935

Text-figure 5

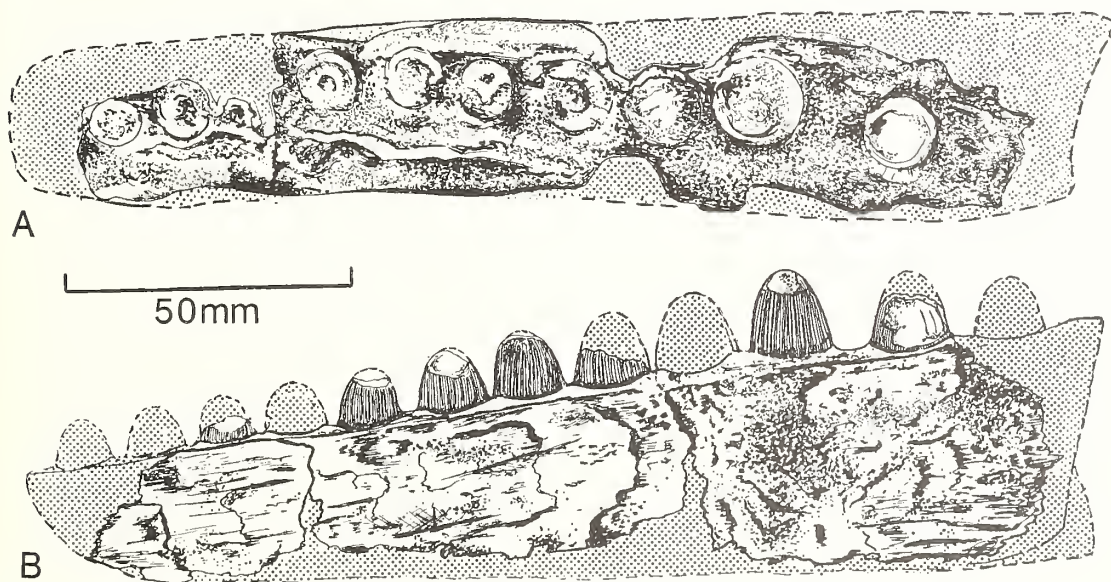
Etymology. Genus named after the village of Igdaman, near to which the specimen was found.

Holotype. BMNH R11898, consisting of three poorly preserved fragments of jaw, probably comprising a single specimen, which include two almost complete teeth and the remains of five more, and three tooth bases.

Horizon and locality. Mt Igdaman, near the village of Igdaman (sometimes In Dama), 5° 50', 15° 22'.

Diagnosis. Massive dentary with dome-shaped unwaisted very finely striated teeth; ?anterior and posterior carina on teeth, sub-circular cross-sections.

Description. R11898, a right dentary, is massively proportioned (Text-fig. 5). Medially, a shallow recess indicates the groove for the splenial. There are seven teeth in various states of preservation (plus three tooth sockets) progressively increasing in size in an anteroposterior direction, except for the last, which is slightly smaller than the penultimate of the preserved teeth. The teeth are straight broad cones with rounded domed tips. The signs are that carinae are present but poor preservation makes this hard to confirm. In cross section the teeth are subcircular. Tooth crowns have unwaisted bases and are covered by fine parallel ribbing or striae, approximately 65–70 per tooth. The largest tooth is approximately 27.2 mm high and 22.5 mm wide at the base. The tooth form is clearly uniform along the entire segment of jaw (Text-fig. 5).



TEXT-FIG. 5. Right dentary of *Igdamanosaurus*. A, dorsal view. B, medial view.

Discussion. Two unusually small foramina for the exits of the mandibular nerve are distinguishable on the lower lateral surface of the dentary. Absence of dentary material in *Globidens* precludes any comparison, although there are similar, relatively small foramina in a maxilla of the holotype of *G. alabamaensis* (Gilmore 1912, pl. 39).

The broad domed teeth, unconstricted at the base, and parallel fine striations of R11898 are unusual for the *Globidentini* (cf. *G. alabamensis* Gilmore 1912, *G. dakotaensis* Russell 1975). The

teeth of R11898 on the other hand show some resemblance to those of '*G.*' *timorensis* (Huene 1935), but even more to the teeth of '*G.*' *aegyptiacus* (Zdanski 1935, pl. 2). The sharing of such an unusual tooth morphology by R11898 and '*G.*' *aegyptiacus* suggests that they should be included in the same genus. The status of '*G.*' *aegyptiacus*, however, was questioned by Russell (1975, p. 240). 'These teeth are quite unlike those in the type skull of *G. alabamaensis* and *G. dakotaensis*, and could belong to an unrecognized genus of durophagous mosasaur'. In view of this, it seems appropriate now to erect a new genus, *Igdamanosaurus*, for the reception of R11898 and '*G.*' *aegyptiacus*.

Russell (1967, p. 144) considered *Globidens* a derivative form of *Clidastes* but 'because of the highly peculiar nature of its spherical teeth', separated the genus into a new tribe of the Mosasaurinae, the Globidentini (Russell 1975). In contrast, vertical striae in *I. aegyptiacus* suggest that it represents an entirely new form of durophagous mosasaur derived from a *Platecarpus*-like ancestor and the genus is consequently assigned to the subfamily Plioplatecarpinae.

Subfamily PLIOPLATECARPINAE
cf. ?*Angolasaurus* Antunes, 1964

Test-figure 6

Referred material. Four vertebrae, BMNH R11901, R11902, R11903, R11904, of varying sizes, the smallest representing an immature individual. Mt Igdaman.

Description. R11901 is a well preserved almost complete cervical vertebra (Text-fig. 6A–C) which in general configuration compares with *Angolasaurus bocagei* (Antunes 1964, pl. 22). The neural spine is very narrow, with well preserved anterior and posterior zygapophyses. The lateral edges of the anterior zygapophyses extend smoothly on to the transverse processes. Distally, the synapophyses are not preserved, but the bases indicate that they were dorsoventrally compressed. Condyles and cotyles are shallow, approximately heart-shaped with the dorsal surfaces depressed slightly, as in *Platecarpus*. The lateral configuration of the hypapophyseal peduncle is similar to that of *A. bocagei* and *Platecarpus*, with the ventral surface sub-circular (Antunes 1964, pl. 22, fig. 1b, c). However, unlike *A. bocagei*, zygosphenes are not observed in R11901, although relatively poor preservation in this part of the vertebra makes identification inconclusive.

R11902 (Text-fig. 6D) is a small, fragmentary cervical vertebra probably belonging to an immature individual; it is in general similar to R11901. The main difference (which may be ontogenetic) lies in the hypapophyseal peduncle, which is not as deep as in R11901 but much broader laterally, spanning almost the entire length of the centrum. The ventral surface of the peduncle unlike that of R11901 is concave rather than convex. The cotyles seem to be fairly flat, but may be exaggerated because of weathering. Specimens R11903 and R11904 (Text-fig. 6E, F) are posterior cervical or early dorsal vertebrae. The main differences from R11901 and R11902 lie in the anteroposterior rather than dorsoventral flattening of the synapophyses. All the above vertebrae show strong cartilaginous articulations (indicated by pitting), suggesting a possible immature state of development.

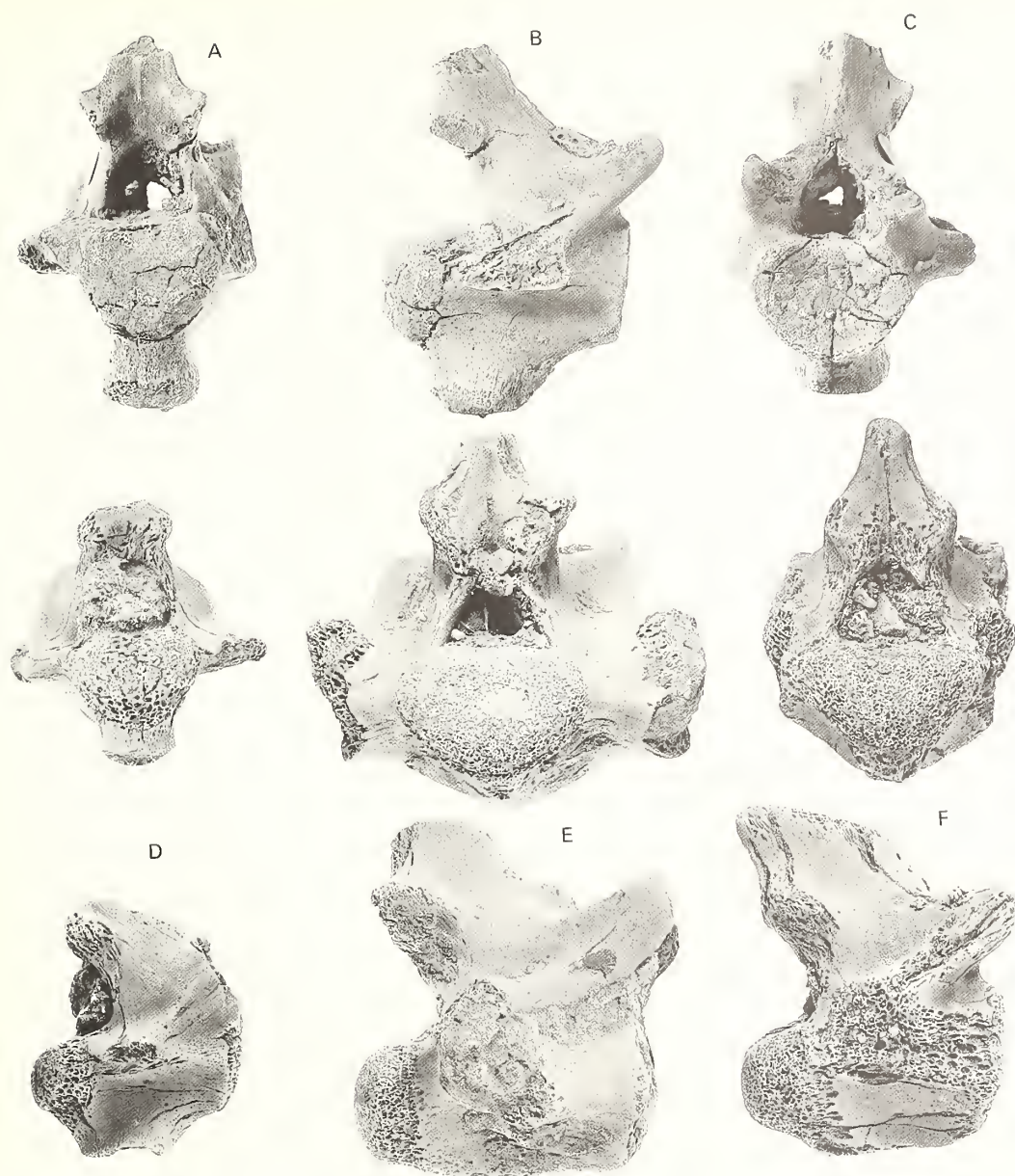
Discussion. The vertebrae of *Angolasaurus* share broad similarities with those of *Platecarpus*, consistent with other characters that the two genera have in common: very large suprastapedial process of the quadrate, deep groove or foramen for basal artery on basioccipital, long striated teeth, and elliptical or heart-shaped articulations of centrum and free haemal spines. For the present, the above characters clearly suggest that *Angolasaurus* should be referred to the subfamily Plioplatecarpinae and not, as indicated by Antunes (1964, p. 164), to the Mosasaurinae.

Subfamily PLIOPLATECARPINAE
Genus *Halisaurus* Marsh, 1869

Halisaurus sp.

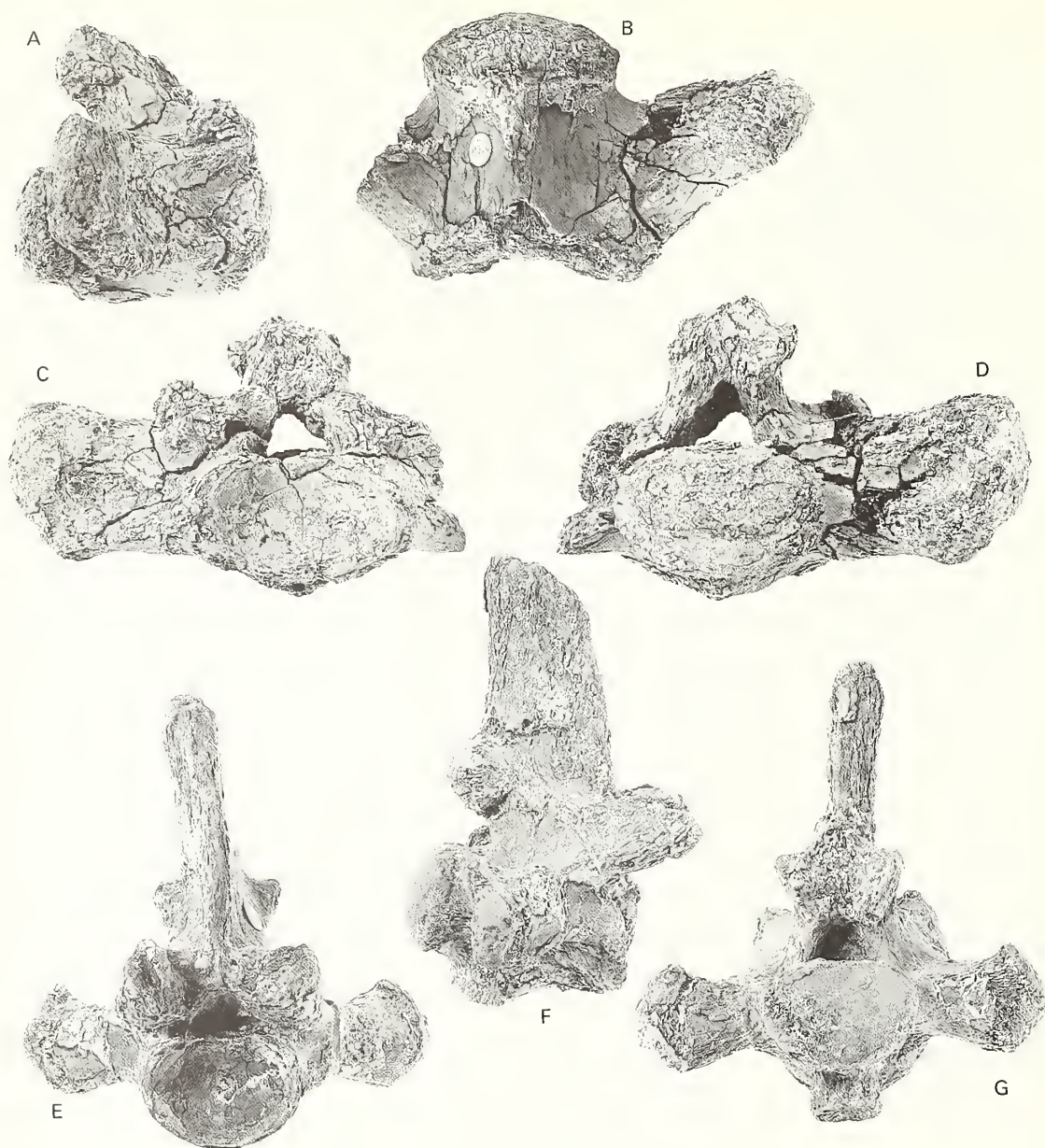
Text-figure 7A–D

Referred material. Vertebrae, BMNH R11983, R11906, R11951 and R11952. Mt. Igdaman.



TEXT-FIG. 6. *Angolasaurus* anterior cervical vertebrae. A, B, C, R11901, posterior, lateral, and anterior views. D R11902, small anterior cervical vertebra. E, F R11903, 11904 posterior cervical or early thoracic vertebrae. D, E, F in anterior (top) and lateral (bottom) views. $\times 1$.

Description. R11923 (Text-fig. 7A–D) is an anterior dorsal, or possibly posterior cervical, vertebra. Much of the neural spine and left synapophysis are absent. The right synapophysis is stout, considerably longer than in other mosasaurs, and situated posteriorly on the centrum. The only preserved posterior zygapophysis is moderately weak. Characteristically, the neural canal is large and the condyle and cotyle nearly twice as wide as deep, nearly kidney bean-shaped with a slight emargination dorsally. There is no evidence of zygosphenes or zygantra.



TEXT-FIG. 7. A-D, *Halisaurus* vertebra (BMNH R11983). A, lateral view; B, ventral view; C, anterior view. D, posterior view. $\times 0.5$. E-G, *Plioplatecarpus* sp. (BMNH R11984). E, anterior view; F, lateral view; G, posterior view.

Discussion. R11951, 11952, and 11906 are the smallest known *Halisaurus* vertebrae (cf. Bukowski 1984; table 1). They are placed in the genus *Halisaurus* on the basis of the characteristically flattened condyles and cotyles, although the problem of identification is augmented here by small size coupled with the generally primitive nature of *Halisaurus* vertebrae (Bukowski 1984). For instance, the relatively large neural canal and relatively broad span across the zygapophyses generally accord with conditions seen in less highly modified squamate families. However, a somewhat less

pronounced state of these features in R11923, R11951, R11952 suggests that the vertebrae belong to *Halisaurus*.

Halisaurus was poorly known, being represented by isolated remains, mainly vertebrae and a few fragments of skull, until Russell (1970) assigned '*Clidastes*' *sternbergi*, a complete skeleton in the University of Uppsala) to the genus. Until it is studied in detail, '*C.*' *sternbergi* is excluded from consideration of *Halisaurus*.

In a label in the IRSNB, Russell referred the Belgian mosasaur *Phosphorosaurus ortliebi* (IRSNB R34, formerly 4671; Dollo 1889), in my view correctly, to *Halisaurus*. It seems that this assignment was based on the similarity of the frontal of IRSNB R34 to that described by Baird and Case (1966, p. 1212), which they indicated had been identified by Russell as *H. platyspondylus*. In contrast, IRSNB R34 and '*C.*' *sternbergi* differ in the size and the position of the parietal foramen. In IRSNB R34 the parietal foramen is relatively large, approximately 24 mm in diameter (Dollo 1889b, pl. 9, fig. 6), one of the largest in the Mosasauridae, and it is situated on the fronto-parietal suture and partly on the frontal. On the other hand, in *C. sternbergi*, 'the foramen parietale is small and lies on the boundary between the first and second third of the parietale, thus considerably further back than in *Clidastes velox* and other mosasaurians' (Wiman 1920, p. 14, fig. 3). These differences in the size and position of the parietal foramen suggest that *Halisaurus* and '*C. sternbergi*' may not belong in the same genus. Estes *et al.* (1988, pp. 148–149) and Lingham-Soliar and Nolf (1989) discuss the apomorphic nature of these characters in squamates and mosasaurs respectively. Provisional assignment of *Halisaurus* to the subfamily Plioplatecarpinae, indicated in a previous cladistic analysis (Soliar 1988), is retained.

Subfamily PLIOPLATECARPINAЕ

Plioplatecarpus Dollo, 1882

Plioplatecarpus sp.

Text-figures 7E–G, 8A–D

Referred material. Fairly well preserved mid-cervical vertebra, BMNH R11924. Mt Igdaman. A posterior caudal vertebra, BMNH R11982. Numerous vertebrae probably belonging to a single specimen, BMNH R11950. In Tahout, top half of '*Mosasaurus* Shales'.

Description. R11924 (Text-fig. 7E–G) consists of a complete fairly well preserved vertebra probably from the mid-cervical vertebral region. The anterior and posterior zygapophyses are well developed. The neural canal is large, tall, and moderately broad and the neural spine posteriorly directed. A fairly slender hypapophyseal peduncle is situated on the posterior ventral surface of the centrum. The peduncle is sub-circular in cross-section. Synapophyses are quite slight and short with the dorsal surface continuing smoothly onto the anterior zygapophyses. The articulating surfaces of the centrum show the characteristic elliptical shape of cervical and early trunk vertebrae found in members of the genus *Plioplatecarpus*, the width approximately one and a half times the depth.

The caudal vertebra (R11922, Text-fig. 8A) is poorly preserved, with most of the neural spine, the left transverse process, and the distal tip of the right transverse process absent. The shape of the condyle is markedly hexagonal. Haemal peduncles indicate the presence of free haemal spines which characterise plioplatecarpines and tylosaurines. The size of the specimen (unless it represents an immature individual) and the sharply defined hexagonal configuration of the condyle, confirm assignment to *Plioplatecarpus* rather than to *Tylosaurus*. R11950 (Text-fig. 8B–D) represents a series of partly articulated vertebrae from different parts of the vertebral column (Text-fig. 8B–D). All show the characteristic vertebral conditions described above.

Discussion. R11924, R11922 and R11950 are to my knowledge the first record of *Plioplatecarpus* from the African continent. However, among poorly preserved undescribed material (GSN 1928–1929) from the Dukamaje Formation of Gilbedi, Nigeria), a cervical vertebra R11954 and a well preserved caudal vertebra showing free haemal peduncles, probably belong to a plioplatecarpine mosasaur. A part of the lower jaw and several fragments of vertebrae may also be plioplatecarpine but are too poorly preserved and gypsiferous to permit assignment.



TEXT-FIG. 8. *Plioplatecarpus* vertebrae (top to bottom), anterior, posterior, and ventral views. A, caudal (R11922). B, anterior cervical (R11950). C, D, lumbar and posterior lumbar respectively (11950). E, F, ?*Platecarpus* lumbar vertebra (R11899); E, posterior view; F, anterior view; G, lateral view. $\times 0.5$.

Subfamily PLIOPLATECARPINAE
Genus *Platecarpus* Cope, 1869

?*Platecarpus* sp.

Text-figure 8E–G

Referred material. BMNH R11899, a fairly well preserved dorsal vertebra with most of the neural spine absent. Mt Igdaman.

Description. R11899 (Text-fig. 8E–G), although otherwise well preserved, lacks its neural spine from a point a few centimetres above the zygapophyses. The span and robustness of the anterior and posterior zygapophyses, suggest that the vertebra belongs to the anterior trunk series. The inflated heart-shaped condyles and cotyles, and the general configuration of the vertebra, suggest that it may be referable to *Platecarpus*.

Subfamily MOSASAURINAE
Mosasaurus Conybeare, 1822
cf. *M. hoffmanni* Mantell, 1829

Text-figure 9E

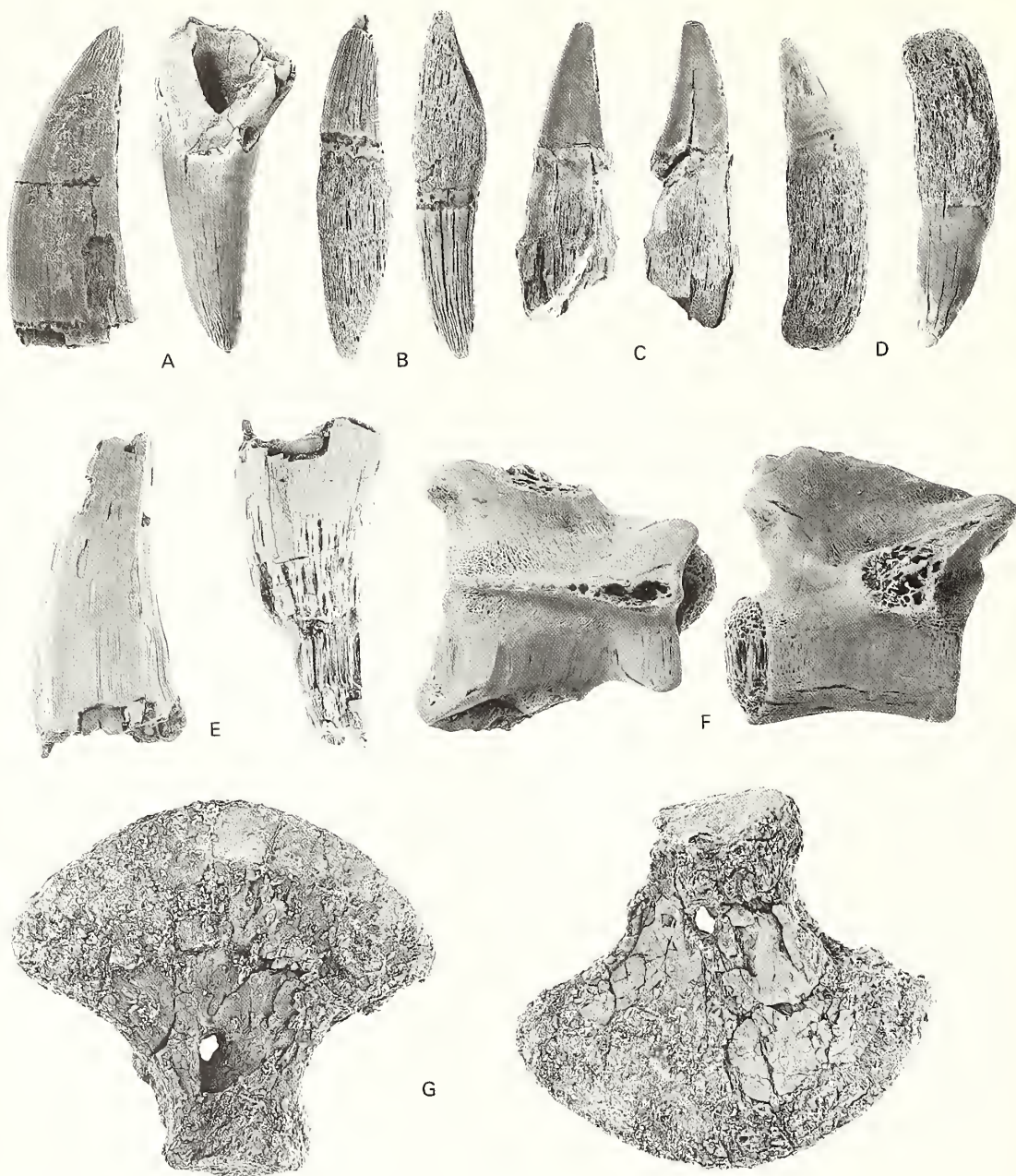
Referred material. BMNH R11913, a fragment of a large tooth crown. Mt Igdaman.

Description. The distal tip and part of the anteroventral surface of the tooth crown are absent (Text-fig. 9E). The specimen is abraded, but shows distinct signs of enamel. The buccal face is divided into five vertical prisms. On the lingual surface, however, owing to weathering, it is not possible to discern prisms with confidence, although this is difficult even in well preserved specimens of *M. hoffmanni* (i.e. the holotype skull and IRSNB 26 and 'R12'). In cross section the tooth shows a fairly deep lingual and slightly rounded buccal surface. Posterior and anterior carinae are present. The tip of the tooth appears to have been gently posteriorly recurved.

Discussion. The tooth probably belongs to *M. hoffmanni*, representing a middle-posterior tooth on the dental ramus, although there is some resemblance to teeth found in larger examples of *M. lemmoulii*, especially in the slight beading present between a few of the facets. At any rate the tooth is referable to *Mosasaurus* judging from the external facets, the cross section, and the shape of the tooth in general.

R11913 represents an important find because it is the first tooth from Niger or Nigeria that can be positively identified as *Mosasaurus*. Swinton's (1930) referral of a tooth from the Dukamaje Formation of Gilbedi to *M. nigeriensis*, is based on insufficient diagnostic characters for the genus (there are no descriptions of facetting or provision of cross-sections).

The literature on mosasaur dentition is sparse, the most significant papers being Edmund (1960) and Russell (1967). A problem in mosasaur classification is the erection of species based on single tooth crowns. Mosasaur teeth manifest certain changes along the tooth row, simple variations of shape and in the nature of tooth facets. This was noted by Leidy (1865, p. 56; pl. 9. fig. 3) and Thevenin (1896, fig. 3, p. 904). Despite this, variation seems to have been ignored by certain authors. For instance, Persson (1959) identified a tooth from Scania as *M. hoffmanni* and subsequently (1963) re-identified it as a new species, *M. ivoensis*, based on what appears to have been a larger number of tooth facets with slightly more concave rather than convex surfaces (conceivably *M. lemmoulii*). Another species, *M. beaugei*, was diagnosed by Arambourg (1952, p. 282–283, pl. 31) on similarly dubious grounds. His description included a variation in tooth shape in an anteroposterior direction. Following this, *M. beaugei* was identified by Price (1957) from the Gramame Formation, in Brazil.



TEXT-FIG. 9. Mosasaur teeth, buccal and lingual views. A (R11896), B (R11949), C (R11894), D (R11985), E (R11913), *Mosasaurus* cf. *hoffmanni*. $\times 1$. F, mosasaur vertebra (R11907), dorsal and lateral views. $\times 2$. G, mosasaur coracoid, lateral and medial views. $\times 0.5$.

Mosasaurinae or Tylosaurinae indet.

Text-figures 9A–D, F, G

Referred material. Three jaw fragments probably representing the same specimen, and including a large tooth

base, BMNH R11914 (Kehehe); teeth R11986, R11949, R11894, R11895 (Igdaman); two large disassociated vertebrae, BMNH R11917 and R11918 (Kehehe); a very small vertebra R11907; a coracoid R11919 and a radius R11931 (Igdaman).

Description. R11914 consists of three poorly preserved fragments of jaw, probably from a maxilla, which appear to represent a single specimen. Associated with one of the fragments is a large tooth base including the jagged remains of the basal part of a tooth crown. This specimen represents the largest mosasaur jaw found in Africa. A BMNH cast of part of the maxilla of the huge holotype skull of *M. hoffmanni* (original in the Paris Museum), described by Cuvier (1834, 1836), is of almost identical proportions, and it permits an estimate of the length of the entire skull of R11914 as approximately 1.4 m.

The largest of the teeth, R11896 (Text-fig. 9A), is approximately 43 mm long and 19.7 mm wide at the base. It is posteriorly recurved with sharp anterior and posterior carinae, extending almost the entire length of the tooth. The surface is enamelled and bears no evidence of striae or facets. The size of the tooth, its general configuration, and lack of strong prisms or facets indicate that it might be tylosaurine. The rest of the teeth, R11949, R11894 and R11895 (Text-fig. 9B-D) are not as well preserved, but are probably mosasaurian.

Two very large vertebrae, R11917 and R11918 from the lower levels of the Dukamaje Formation, clearly come from a very large mosasaur with the proportions of R11914. Large vertebral material mentioned previously in the literature by various authors (Swinton 1930; Azzaroli *et al.* 1975; Soliar 1988), as well as previously undescribed material from Kaffe and Gilbedi, is similarly impregnated with a matrix of yellow marl as is R11914, possibly indicating a similar horizon for all specimens.

R11907 (Text-fig. 9F) represents probably the smallest mosasaur vertebra known, clearly belonging to an immature individual or hatchling. It belongs to the lumbar series, and the general configuration suggests that it is mosasaurian. The neural spine is absent. Articulating surfaces are heart-shaped, deeper than wide. Slight pinched depressions on the anterodorsal surfaces of the vertebra on either side of the neural spine may indicate the inception of zygosphenes in a very young individual.

R11919 (Text-fig. 9G) is a fairly well preserved coracoid, the first record of a mosasaur pectoral element in Africa. It lacks an emargination of the distal border and the coracoid foramen is moderate in size. The small size of the specimen indicates that it may belong to an immature individual or a small taxon such as *Clidastes*. R11931 is a large fragment of a radius, but no further distinction is possible.

PALAEOECOLOGY OF MOSASAURS OF THE IULLEMMEDIN BASIN OF NIGER

In the south-western part of the Iullemmedin Basin, Petters (1979*b*, p. 950) defined four marginal environments, marshes, lagoons, estuaries, and epeiric seas. These were based upon computed alpha diversity values for the Dukamaje benthic foraminiferan assemblages and on the preponderance of the arenaceous foraminifera *Miliammina*, *Haplophragmoides*, *Trochammina*, and *Ammobaculites*, which indicates adaptation to stress and marginal environments.

The environments suggested for particular mosasaurs are: *Mosasaurus* (coastal waters); ?*Platecarpus* (open sea); *Plioplatecarpus*? (deep water) (Russell 1967); *Halisaurus* (unknown); *Goronyosaurus*, *Angolasaurus*, and *Igdamanosaurus* (coastal waters and lagoons).

If Petter's interpretation of the environment of the south-western Iullemmedin Basin is correct, then the presence of suggested open-sea forms of mosasaurs such as *Platecarpus* and deep-water divers such as *Plioplatecarpus* may appear inconsistent. There is, however, very little evidence in the literature to corroborate these interpretations of the lifestyle of *Platecarpus* and *Plioplatecarpus*. Russell (1967) has shown there to be no especial significance in the tympanic membrane for example in diving. A calcified tympanic membrane in fact occurs widely in most mosasaurs, being present in members of all three subfamilies (Williston 1898; Russell 1967).

Among mosasaurs, the unique presence of enclosed olfactory lobes in *Goronyosaurus* is puzzling. The enclosed condition of the lobes in the Varanoidea (Mertens 1942) is regarded as a synapomorphy by Estes *et al.* (1988), but is not normally present in mosasaurs. The enclosed condition in *Goronyosaurus* may be associated with more highly developed olfactory lobes and sense of olfaction. This is consistent with other features of the genus that suggest an efficient detection of hidden prey; for example, the high number of large foramina on the premaxilla which suggest an array of large nerve endings to an apparently highly sensitized snout. Either condition would have been particularly useful for hunting in the quiet murky waters of sheltered bays and estuaries and



TEXT-FIG. 10. *Goronyosaurus nigeriensis* (IGF 14750). A, lateral view. B, dorsolateral view. $\times 0.3$.

in preying upon hidden young of marine fauna including perhaps those of mosasaurs (Russell 1967, pp. 1, 65). Further, the very small eyes of *Goronyosaurus* (relatively perhaps the smallest in the Mosasauridae) suggest that *Goronyosaurus* did not rely heavily on vision.

Modern-day analogues of this kind of predation are seen in varanids which search out hidden prey by 'specialized chemoreception' followed by 'rapid, skilful capture' (Losos and Greene 1988, p. 379). These authors suggest that this is a derived condition in varanids, a view that may hold equally true for mosasaurs.

Igdamanosaurus is the first record in the Mosasauridae of a predator complying with Massare's (1987) tooth morphotype in the 'crunch' guild. This contrasts with the 'crush' guild in which she placed *Globidens*. From an ecological perspective, *Igdamanosaurus* probably occupied a feeding mode somewhere between *Prognathodon* (Lingham-Soliar and Nolf 1989) and *Globidens* (Russell 1967), subsisting presumably on a diet of moderately soft-shelled invertebrates.

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Dedication. This paper is dedicated to the memory of Beverly Halstead who made the dreams of dragons a wonderful reality for me.

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ISOLATED GRAPTOLITES FROM THE LLANDOVERY OF KALLHOLEN, SWEDEN

by D. K. LOYDELL

ABSTRACT. A graptolite fauna of *Monograptus argenteus* Biozone age (Aeronian = Middle Llandovery), chemically isolated from limestone nodules formerly thought to be of *M. turriculatus* Biozone age (Telychian = Upper Llandovery), is described. The total fauna comprises *Metachimacograptus hughesi* (Nicholson), *Glyptograptus* aff. *incertus* Rickards, *G. sinuatus sinuatus* (Nicholson), *Clinochimacograptus retroversus* Bulman and Rickards, *Agetograptus primus* Obut and Sobolevskaya, *Agetograptus* sp., '*Orthograptus*' *cyperoides* (Törnquist), '*O.*' *insectiformis* (Nicholson), *Monoclimacis* sp., *Pristiograptus concinnus* (Lapworth), *Pribylograptus leptotheca* (Lapworth), *Monograptus communis communis* Lapworth, *M. denticulatus sensu* Sudbury, *M. millepeda* M'Coy and *Rastrites peregrinus* Barrande. Spines are recognized for the first time on the thecae of *M. c. communis* and *M. millepeda*. It is suggested that *M. lobiferus* evolved from *M. millepeda* which had itself evolved from *M. c. communis*. The generic diagnosis for *Pribylograptus* Obut and Sobolevskaya is emended, as the existing diagnosis for the genus is based upon a misinterpretation of the thecal structure derived from examination of pyrite internal moulds.

IN 1970, Hutt, Rickards and Skevington described a number of graptolites (eleven species in total) chemically isolated from limestone nodules from the *turriculatus* Biozone of Osmundsberget, Dalarna, Sweden. When similar material, collected by Drs M. G. Bassett, R. B. Rickards and J. Gluyas became available, it seemed an ideal opportunity to compare uncrushed, isolated material with the common low-relief internal moulds and rare flattened rhabdosomes found in Wales. Such study would aid interpretation of, in particular, the thecal structures of such imperfect material.

Dr Bassett also provided limestone nodules from Kallholen (also in Dalarna), which were considered (pers. comm.) to come from a similar horizon to the Osmundsberget nodules. However, the recognition of species such as *Monograptus millepeda* (M'Coy, 1850) and *Pribylograptus leptotheca* (Lapworth, 1876) in the residues of some of the first samples processed indicated that this was not the case, and that the Kallholen nodules contained a fauna from rather earlier in the Llandovery, from the Aeronian *M. argenteus* Biozone.

The vast majority of the species extracted from these nodules have never before been described in isolated condition and thus a large amount of new (and often surprising) morphological information, in some cases of considerable taxonomic importance, has been derived.

TECHNIQUES

The isolation techniques used are fully described in Dumican and Rickards (1985) and in Bates *et al.* (1988). The nodules were dissolved in acetic acid as this has a less effervescent reaction with carbonate than hydrochloric acid, and thus causes less damage to emerging specimens. Some specimens were cleared (i.e. rendered transparent) using the technique described by Berry (pp. 106–107, in Kummel and Raup 1965). Initial examination under a light microscope was followed by more detailed study with a scanning electron microscope (SEM) again using the techniques described in Dumican and Rickards (1985).

PREVIOUS WORK ON ISOLATED NON-RETIOLITE LLANDOVERY GRAPTOLITES

Any retiolite graptolites isolated from the nodules were passed to Drs Bates and Kirk. The following account of previous research therefore considers only monograptids and 'normal' diplograptids.

Other than Hutt, Rickards and Skevington's (1970) work, which also included descriptions of seven species from the *Coronograptus gregarius* Biozone (Aeronian) of Silbberg, also in Dalarna, Sweden, little work has been published on isolated non-retiolite Llandovery graptolites, although undoubtedly a wealth of material exists, particularly from the Canadian Arctic. This dearth of studies is surprising, for as Fortey (1989) states: 'One good isolated fossil fauna is worth any amount of speculation on structure and phylogenetics based on flattened specimens.'

Bulman (1932) described three monograptid species from the *Retiolites*-Shales of Stygforsen, Dalarna, Sweden, which had been prepared by Holm in the latter part of the nineteenth century. Two of these he assigned to *Monograptus priodon* (Bronn, 1835) and *M. spiralis* (Geinitz, 1842). The third he was unable to identify. It is herein recognized as *Streptograptus grayae* (Lapworth, 1876).

Lenz (1974) analysed evolutionary trends within *M. priodon* from the uppermost Llandovery to lower Wenlock, using isolated material from Cornwallis Island, Arctic Canada.

Paškevičius (1976) erected the genus *Lithuanograptus* on the basis of examination of isolated Rhuddanian and Aeronian diplograptaceans from Lithuania, USSR. It is probable that many of his specimens are simply flattened metaclimacograptids.

In 1977, Rickards, Hutt and Berry illustrated thecae considered by them to be from *M. delicatulus* Elles and Wood, 1913. Crowther (1981) described *Paraclimacograptus innotatus innotatus* (Nicholson, 1869) from the Dergaish River, south Ural Mountains, USSR, and *Dimorphograptus?* sp. from Cornwallis Island, Canada.

Obut and Sennikov (1980) described a number of *Monograptus triangulatus* Biozone (Aeronian) monograptid and diplograptid taxa from the Siberian Platform, USSR. Their fine material would certainly benefit from further examination with an SEM.

Bates and Kirk (1984) gave a description and discussed the probable function of ancoras from three different diplograptid species. Their suggestion of horizon as ? *M. turriculatus* Zone for this Kallholen material is, as mentioned above, now known to be incorrect.

Melchin and Lenz (1986) described *M. turriculatus* (Barrande, 1850) from Cornwallis Island, and discussed its possible derivation from *M. sedgwickii* (Portlock, 1843). Chen (1986a) described seven generally poorly preserved species from the Aeronian of Yichang, W Hubei, China. This material was extracted from siliceous marl concretions by dissolution first in hydrochloric and then hydrofluoric acid. Chen (1986b) has also described isolated material of *Streptograptus plumosus* (Baily, 1871) (misidentified by him as *S. nodifer* (Törnquist, 1881)) from north-east Guizhou, and further work on isolated faunas is in progress.

Most recently, Lenz and Melchin (1989) have described uncompressed specimens of *M. spiralis* again from Cornwallis Island, and suggest that this species is unlikely to be ancestral to the genus *Cyrtograptus* Carruthers, 1867, three isolated species of which they also describe – *C. sakmaricus* Koren, 1968, *C. sp.* and *C. cf. C. laqueus* Jackson and Etherington, 1969.

LOCALITY INFORMATION

As Kallholen has not been visited by the author, the information below is derived entirely from Bassett (pers. comm. to D. Bates).

The graptolites were isolated from nodules from the lowest band exposed (within basal 2 m) in the Llandovery sequence unconformably overlying the Upper Ordovician Boda Limestone. The nodules were collected from sections on both sides of the western entrance to the quarry on the east side of road 296, directly opposite Kallholen limestone works, 7.5 km NE of Orsa Church, Siljan district, Dalarna (UTM Grid reference VH 8440 8153).

SYSTEMATIC PALAEOONTOLOGY

The terminology used is mainly that of Bulman (1970). Thecal spacing is expressed in terms of a two theca repeat distance (2TRD), as defined by Howe (1983).

Synonymies are brief for the well-known taxa, as more complete synonymies may be found in, for example, Rickards (1970) and Hutt (1974, 1975). They are annotated with the symbols proposed by Richter (1948) and Rabien (1954), summarized in Matthews (1973).

Suprageneric classification is based on Mitchell (1987), with reservation, particularly with regard to the lowly status conferred by Mitchell (*op. cit.*) upon the 'monograptids'.

All material figured in the plates is housed in the Institute of Earth Studies, University College of Wales, Aberystwyth.

Repositories of type material are abbreviated as follows: BM (NH) – Natural History Museum; BU – Birmingham University; SM – Sedgwick Museum, Cambridge.

Order GRAPTOLIDEA Lapworth, 1873

Suborder VIRGELLINA Fortey and Cooper, 1986

Superfamily DIPLOGRAPTACEA Lapworth, 1873 (emend. Mitchell, 1987)

Family GLYPTOGRAPTIDAE Fortey and Cooper, 1986

Subfamily GLYPTOGRAPTINAE Fortey and Cooper, 1986

Genus GLYPTOGRAPTUS Lapworth, 1873 (emend. Mitchell, 1987)

Type species. Original designation; *Diplograptus tamariscus* Nicholson, 1868, p. 526, pl. 19, figs 10–13.

Glyptograptus aff. *incertus* Rickards, 1970

Plate 1, fig. 1

- 1970 *Glyptograptus* aff. *incertus* (Elles and Wood, 1907); Rickards pp. 40–41, text-fig. 14, fig. 11.
 p1974 *Glyptograptus* (*G.*) *incertus* (Elles and Wood, 1907); Hutt, p. 25, pl. 3, fig. 3; pl. 4, fig. 13 (*non* 12); text-fig. 8, fig. 11.

Material. One specimen.

Description. The 4.5 mm long specimen has been laterally compressed producing a corrugated appearance along its midline. The thecae have sharp genicula on $th1^1$ – 3^3 . There is then an abrupt change to sigmoidally curved thecae and flowing, rounded genicula. Thecal apertures are horizontal. Dorso-ventral width increases from 0.5 mm at $th1^1$ to 1 mm at $th5^1$. 2TRD ranges from 1.3 to 1.5 mm.

Remarks. The specimen agrees very well with the material illustrated by Rickards (1970) and Hutt (1974). *G. incertus* Elles and Wood, 1907 differs in having a broader, more rounded proximal end and also in that the geniculum becomes less angular more gradually along the length of the rhabdosome. The latter species is fully described by Packham (1962).

Glyptograptus sinuatus sinuatus (Nicholson, 1869)

Plate 1, fig. 2

- *.1869 *Diplograptus sinuatus* Nicholson, p. 235, pl. 11, fig 11.
 1907 *Diplograptus* (*Glyptograptus*) *sinuatus* Nicholson; Elles and Wood, pp. 255–257, pl. 31, fig. 6; text-fig. 175.
 .1970 *Glyptograptus sinuatus sinuatus* (Nicholson); Rickards, pp. 41–42, pl. 4, fig. 1.
 .1974 *Glyptograptus* (*G.*) *sinuatus sinuatus* (Nicholson); Hutt, p. 28, pl. 4, figs 1–4, 10.
 .1975 *Glyptograptus sinuatus sinuatus* (Nicholson); Bjerreskov, p. 31, pl. 4, fig. D.

Holotype. By monotypy; specimen figured Nicholson 1869, pl. 11, fig. 11; from the Llandovery of Skelgill, the English Lake District.

Material. Several proximal ends, and a few more fully developed rhabdosomes.

Description. The rhabdosome increases in width fairly rapidly from 0.5–0.6 mm at $th1^1$ to 1.3 mm at $th5^1$. 2TRD is 1.35–1.5 mm at $th2^1$, and 1.5–1.55 mm at $th5^1$. The first three thecal pairs have sharp genicula and straight supragenicular walls inclined at a very low angle to the rhabdosome axis. An abrupt change in thecal morphology then occurs, all further thecae being sigmoidally curved with flowing genicula.

Remarks. The abrupt change in the thecal morphology has been widely illustrated. This species, perhaps more than any other, illustrates the futility of the traditional diplograptacean generic classification (see Bulman 1970) which was based largely on thecal morphology. The character of the proximal thecae of this species would place it in *Climacograptus* Hall, 1865, whilst that of the distal thecae would place it in *Glyptograptus* Lapworth, 1873. As a result of the work of Fortey and Cooper (1986) and Mitchell (1987) this traditional classification has now been abandoned in favour of one which is phylogenetically based, concentrating on early astogenetic development.

Genus CLINOCLIMACOGRAPTUS Bulman and Rickards, 1968.

Type species. Original designation; *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* Bulman and Rickards, 1968, p. 8; from the Llandovery of Sweden and Britain.

Clinoclimacograptus retroversus Bulman and Rickards, 1968

Plate 1, figs 5 and 14

- 1893 *Climacograptus scalaris* Lin.; Törnquist, pp. 2–6, figs 1–3, 5–8, 11–15, ? 4, 9, 10, 16–22.
- *.1968 *P. (Clinoclimacograptus) retroversus* Bulman and Rickards, pp. 8–12, text-figs 3–5.
- .1970 *Pseudoclimacograptus (Clinoclimacograptus) retroversus* Bulman and Rickards; Rickards, pp. 34–35, text-fig. 14, figs 1–4.
- .1974 *Pseudoclimacograptus (Clinoclimacograptus) retroversus* Bulman and Rickards; Hutt, p. 23, pl. 2, figs 10–12.
- .1975 *Pseudoclimacograptus retroversus* (Bulman and Rickards); Bjerreskov, pp. 25–26, text-fig. 9D, E.

Holotype. Original designation; figured Bulman and Rickards 1968, fig. 4b; SM A52951; from Tomarp Sweden, probably *M. sedgwickii* Biozone.

Material. Approximately 200 specimens.

Description. The rhabdosome is essentially parallel-sided, increasing in dorso-ventral width only very gradually from 0.6–0.8 mm at $th1^1$ to a distal maximum of 1.1–1.35 mm, although some specimens exhibit a slight subsequent reduction in width (as shown by specimen UCWG961B, figured Pl. 1, fig. 14). 2TRD increases from 1.2–1.4 mm at $th2^1$ to 1.45–1.6 mm distally. The thecae have sharp genicula and characteristic slightly concave supragenicular walls. The apertures alternate and are horizontal or very slightly introverted. Their excavations each comprise *c.* one-tenth of the dorso-ventral width for the first thecal pair, increasing to *c.* one-fifth distally. The median septum (seen on cleared specimens) is gently undulating proximally, becoming almost straight distally.

Remarks. The material agrees well with Bulman and Rickards's (1968) description other than in its attainment of a greater distal width. In this respect it resembles *Pseudoclimacograptus (Clinoclimacograptus)? washingtoni* Bjerreskov, 1981, but this latter species has a narrower proximal end and more widely spaced thecae. Bulman and Rickards (1968) noted the long range of *Cl. retroversus* (*M. triangulatus* to *M. sedgwickii* Biozones) and suggested that it might be possible to subdivide it into a number of stratigraphically useful forms.

Genus METACLIMACOGRAPTUS Bulman and Rickards, 1968

Type species. Original designation; *Diplograpsus Hughesi* Nicholson, 1869, p. 235, pl. 11, figs 9 and 10; from the Llandovery of the Lake District, England.

Metaclimacograptus hughesi (Nicholson, 1869)

Plate 1, figs 3, 4, 6, 9, 12

- *.1869 *Diplograpsus Hughesi* Nicholson, p. 235, pl. 11, figs 9 and 10.
- 1906 *Climacograptus Hughesi* Nicholson; Elles and Wood, pp. 208–210, pl. 27, fig. 11; text-fig. 140.
- .1968 *P. (Metaclimacograptus) hughesi* (Nicholson); Bulman and Rickards, pp. 3–6, fig. 1.
- .1970 *Pseudoclimacograptus (Metaclimacograptus) hughesi* (Nicholson); Rickards, p. 33, text-fig. 14, fig. 6.
- .1970 *P. (Metaclimacograptus) hughesi* (Nicholson); Hutt, Rickards and Skevington, p. 4, pl. 1, figs 1–4.
- 1974 *Pseudoclimacograptus (Metaclimacograptus) hughesi* (Nicholson); Hutt, p. 22, pl. 2, figs 6, 7, 13, 14.
- 1975 *Pseudoclimacograptus undulatus* (Kurck, 1882); Bjerreskov, p. 26, pl. 4, fig. E.

Neotype. Designated Přibyl 1948, p. 18, as the specimen figured by Elles and Wood 1906, pl. 27, fig. 11a; BM (NH) P1890.

Material. Several hundred specimens.

Description. The rhabdosome appears essentially parallel-sided, its width increasing very gradually from 0.5–0.6 mm at $th1^1$ to a distal maximum of 0.75 mm. 2TRD is 1.0–1.25 mm at $th2^1$. Distally it lies between 1.2 and 1.5 mm. The thecae have sharp, slightly overhanging and thickened genicula. Their apertures alternate. They are introverted, with excavations comprising c. one-third of the rhabdosome's dorso-ventral width. The medium septum (seen on cleared specimens) undulates.

One specimen has a circular cyst-like growth on the obverse side of the rhabdosome close to the aperture of $th2^1$ (Pl. 1, figs 3 and 6).

Remarks. Bulman and Rickards (1968) describe this species in great detail. The thickening of the geniculum is presumably the same structure as the genicular hood described in this species by Bulman and Rickards (*op. cit.*). Hutt, Rickards and Skevington (1970) noted faint traces of genicular hoods on some of their isolated, but flattened, material.

The cyst-like growth may be the result of parasitism. Similar growths have been recognised before, for example by Jackson (1971). Conway Morris (1981) gives a useful review of parasitism in the fossil record, which includes examples on graptolites.

Subfamily RETIOLITINAE Lapworth, 1973 (emend. Mitchell, 1987)

Genus AGETOGRAPTUS Obut and Sobolevskaya, 1968

Type species. Original designation; *Agetograptus secundus* Obut and Sobolevskaya (in Obut, Sobolevskaya and Merkureva 1968), pp. 79–80, pl. 8, figs 9–12; pl. 9, figs 1–13; pl. 10, figs 1–5; from the Llandovery of a borehole in the Norilsk region, USSR.

Diagnosis. Species with $th1^2$ longer than $th1^1$ and 2^1 so that its aperture is higher than that of $th2^1$. Throughout the rhabdosome the aperture of the thecae of the second series open above the succeeding thecae of the first series.

Remarks. Bulman (1970) placed this genus into synonymy with *Dimorphograptus* Lapworth, 1876. However, it differs from this genus in that in *Agetograptus* $th1^2$ is elongated rather than being suppressed. The superficial appearance of the proximal end is similar in both genera.

Rickards, Hutt and Berry (1977, p. 25) note that some specimens of *Ag. secundus* have a normal proximal end (i.e. thecal apertures alternating). Neither of the species described herein exhibits this feature, however, which Rickards, Hutt and Berry (*op. cit.*) consider as being indicative of a dithyrial population (Jaanusson 1973).

Agetograptus primus Obut and Sobolevskaya, 1968

Plate 1, figs 11, 16, 18, 19; Plate 2, fig. 2

- *.1968 *Agetograptus primus* Obut et Sobolevskaya; Obut, Sobolevskaya and Merkureva, pp. 80–1, pl. 10, figs 6–12.
- 1970 *Orthograptus bellulus* Törnquist; Churkin and Carter, p. 28, pl. 3, fig. 1; text-fig. 12G.
- ?1970 *Orthograptus* cf. *insectiformis* (Nicholson, 1869); Rickards, pp. 46–47, text-fig. 14, fig. 18.
- p1978 *Orthograptus insectiformis* (Nicholson); Chen and Lin, p. 39, pl. 7, fig. 3 (*non* 1 and 2).

Holotype. By original designation, the specimen illustrated by Obut, Sobolevskaya and Merkureva 1968, pl. 10, fig. 6, from the Middle Llandovery of borehole N-1, Norilsk district, USSR.

Material. Approximately 100 specimens.

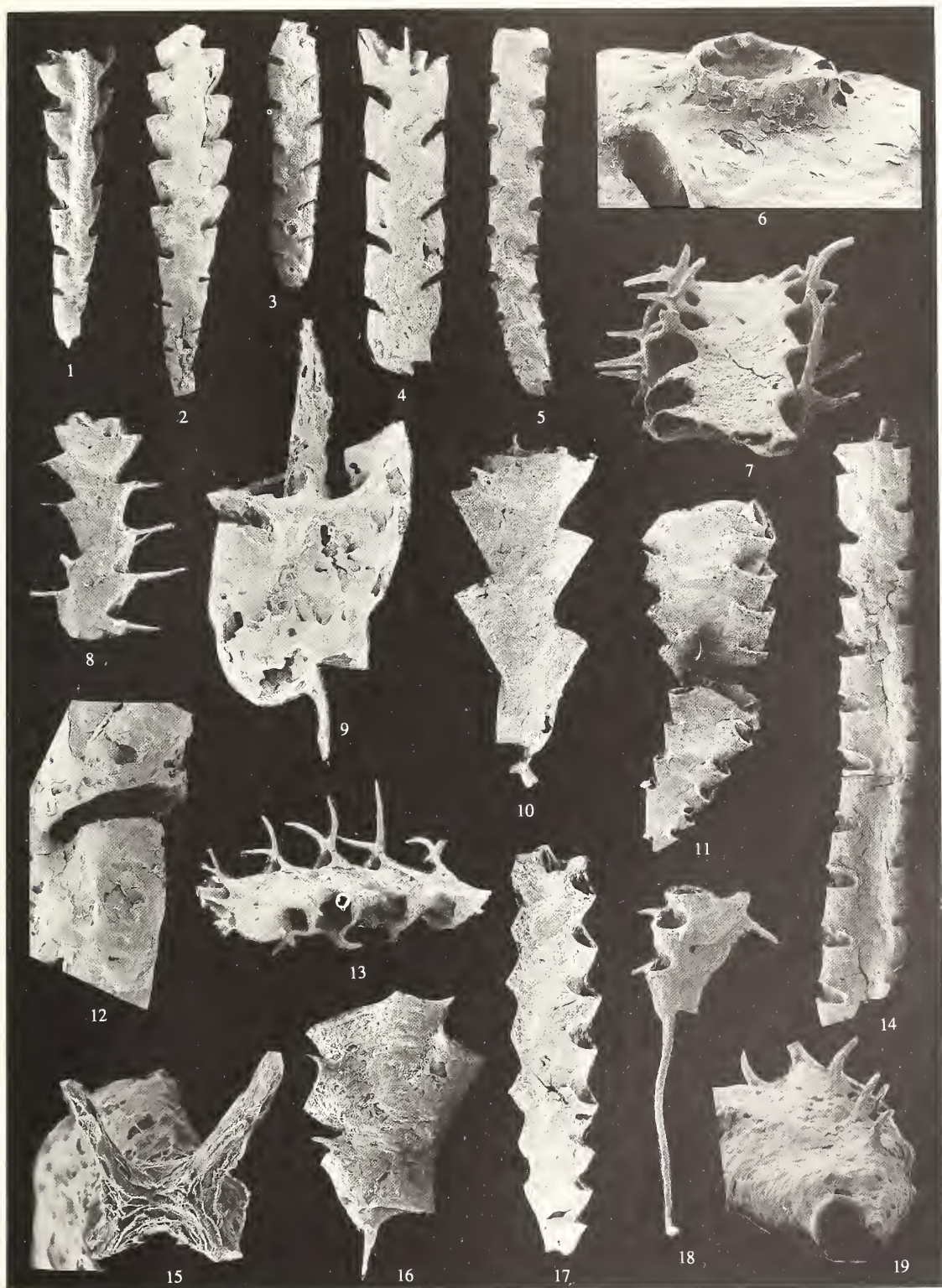
Description. The rhabdosome increases moderately rapidly in dorso-ventral width from 0.4–0.65 mm at th_1^1 to 0.9–1.2 mm at th_5^1 , the maximum distal value recorded being 1.9 mm. 2TRDs are characteristically low, 0.65–0.9 mm at th_2^1 , increasing to 1.15–1.4 mm distally. The thecae are straight tubes inclined at *c.* 30° to the rhabdosome axis. Each aperture bears a pair of short, gently curving spines directed antero- and posterio-laterally. These are situated on the dorsal margin of the aperture. The virgella is long and robust.

Remarks. The position of the spines results in them being visible only when an oblique or lateral view is presented. They were not observed by Obut and Sobolevskaya (1968) in their material.

Poorly preserved specimens of *Ag. primus* might easily be mistaken for '*Orthograptus*' *bellulus* (Törnquist, 1890).

EXPLANATION OF PLATE 1

- Fig. 1. *Glyptograptus* aff. *incertus* Rickards, 1970, UCWG961C, obverse view; note lateral compression, $\times 10$.
 - Fig. 2. *Glyptograptus sinuatus* (Nicholson, 1869), UCWG943B, obverse view, $\times 10$.
 - Figs 3, 4, 6, 9, 12. *Metaclimacograptus hughesi* (Nicholson, 1869), 3, UCWG956B, obverse view; note cyst-like structure adjacent to aperture of th_2^1 , $\times 10$. 4, UCWG919A, obverse view; $\times 20$. 6, UCWG956B, cyst-like structure, $\times 100$. 9, UCWG930D, early growth stage, $\times 50$. 12, UCWG930C, thecal aperture, $\times 75$.
 - Figs 5 and 14. *Clinoclimacograptus retroversus* Bulman and Rickards, 1968. 5, UCWG943A, obverse view; $\times 10$. 14, UCWG961B, distal fragment showing slight narrowing of rhabdosome and decrease in angularity of geniculum, $\times 10$.
 - Figs 7, 8, 13. '*Orthograptus*' *insectiformis* (Nicholson, 1869). 7, UCWG956D, viewed from distal end of rhabdosome, $\times 20$. 8, UCWG956A, mesial fragment, $\times 10$. 13, UCWG956A, showing form of thecal apertures and spines, $\times 15$.
 - Figs 10 and 15. '*Orthograptus*' *cyperoides* (Törnquist, 1897). 10, UCWG1027, reverse view, $\times 20$. 15, UCWG1027, ancora, $\times 150$.
 - Figs 11, 16, 18, 19. *Agetograptus primus* Obut and Sobolevskaya, 1968. 11, UCWG911B, reverse view, $\times 10$. 16, UCWG960D, early growth stage, $\times 40$. 18, UCWG958C, early growth stage; note long, robust virgella, $\times 40$. 19, UCWG911B, view from proximal end; note thecal spines, $\times 20$.
 - Fig. 17. *Agetograptus* sp., UCWG919D, reverse view, $\times 15$.
- All scanning electron micrographs.



LOYDELL, Swedish Llandovery graptolites

Agetograptus sp.

Plate 1, fig. 17; Plate 2, figs 1 and 3

Material. Two specimens.

Description. The rhabdosome is gently tapering. Its dorso-ventral width increases from 0.5–0.55 mm at $th1^1$ to 0.9–1.0 mm at $th5^1$. 2TRD at $th2^1$ is 0.75 mm. At $th5^1$ it is 1.1 mm. The thecae are simple tubes, inclined at c. 25° to the rhabdosome axis, with slightly everted thecal apertures. The nema is partially enclosed in a sheath-like structure (Pl. 2, fig. 1).

Remarks. This species is similar to *Ag. tenuilongissimus* Obut and Sobolevskaya, 1968 but has more closely spaced thecae.

Genus 'ORTHOGRAPTUS' Lapworth, 1873

'*Orthograptus*' *cyperoides* (Törnquist, 1897)

Plate 1, figs 10 and 15

- *.1897 *Diplograptus cyperoides* Törnquist, p. 16, pl. 2, figs 30–32.
- 1907 *Diplograptus* (*Orthograptus*) *cyperoides* Törnquist; Elles and Wood, pp. 238–239, pl. 29, fig. 8; text-fig. 158.
- 1970 *Orthograptus cyperoides* (Törnquist); Rickards, pp. 45–46, text-fig. 14, figs 12 and 17.
- ?1974 *Orthograptus cyperoides* (Törnquist); Hutt, p. 35, pl. 6, figs 2–5; text-fig. 9, figs 6 and 7.
- ?1975 *Orthograptus cyperoides* (Törnquist); Bjerreskov, pp. 28–29, text-fig. 10D.
- .1985 *Orthograptus cyperoides* (Törnquist); Storch, p. 90, pl. 1, figs 1–4, (? 5); text-fig. 2F, G.

Type specimen. Not yet designated. Törnquist's material was from the *cometa* Biozone of Tomarp, Sweden.

Material. One specimen, a proximal end, bearing thecae up to $th3^1$.

Description. The specimen has a width of 0.8 mm at $th1^1$ and 0.9 mm at $th2^1$. The simple thecae are inclined at 30° to the rhabdosome axis and have apertures almost perpendicular to the thecal axis. A median septum is not present. The virgella divides a short distance from the sicula aperture into four branches, all of which are broken.

Remarks. The dimensions of the specimen agree well with previous descriptions. Both Hutt (1975) and Bjerreskov (1975) noted thecal apertural spines, prolonged into a fine network in the case of the latter's material, on some of their specimens of this species. Štorch (1985), however, observed no such spines, but did note a virgellar meshwork, often covered with a membrane, on about half of his flattened specimens.

Hutt (1975) suggested that *Orthograptus cyperoides* and *O. insectiformis* might be conspecific. The present material of the two species illustrated herein would indicate that this is probably not the case.

'*Orthograptus*' *insectiformis* (Nicholson, 1869)

Plate 1, figs 7, 8, 13

- *.1869 *Diplograptus insectiformis* Nicholson, p. 237, pl. 11, fig. 13.
- .1907 *Diplograptus* (*Orthograptus*) *insectiformis* Nicholson; Elles and Wood, pp. 228–229, pl. 28, fig. 7; text-fig. 150.
- 1970 *Orthograptus* ? sp.; Hutt, Rickards and Skevington, p. 5, pl. 1, figs 8–10.
- .1974 *Orthograptus insectiformis* (Nicholson); Hutt, pp. 34–35, text-fig. 9, figs 1–3, 13.
- .1974 *Orthograptus insectiformis* (Nicholson); Rickards and Koren, pp. 200–201, figs 1–4.
- .1975 *Orthograptus insectiformis* (Nicholson); Bjerreskov, p. 29, text-fig. 10c.

Holotype. By monotypy; specimen figured by Nicholson 1869, pl. 11, fig. 13; BM (NH) Q3113; from the Llandovery of Dob's Linn, Moffat, Scotland.

Material. Approximately 20, mostly fragmentary, specimens.

Description. The rhabdosome increases in dorso-ventral width (excluding spines) from 0.7–0.8 mm at th1¹ to a maximum of 1.2 mm. 2TRD distally is 1.4 mm. The thecae are simple straight tubes with horizontal apertures each of which is furnished with two pairs of gently curved spines (up to 0.75 mm long) directed antero- and postero-laterally. The sicula bears an ancora of type 3 of Bates and Kirk (1984).

Remarks. The ancora of this species has been described and its possible function discussed by Bates and Kirk (1984).

'*Orthograptus*' *inopinatus* Bouček, 1943 is very similar in its dimensions to '*O.*' *insectiformis*. It differs in its possession of spines projecting from the nema (see illustrations in Štorch 1985).

Subfamily MONOGRAPTINAE Lapworth, 1873

Genus MONOCLIMACIS Frech, 1897

Type species. Original designation; *Graptolithus vomerinus* Nicholson, 1872, emend. Lapworth; from the Coniston Flags of northern England.

Diagnosis. Thecae geniculate, with straight supragenicular walls approximately parallel to the rhabdosome axis. Proximal apertures may be hooked or bear lateral lappets; distal apertures often simpler, of climacograptid appearance, sometimes with genicular hoods.

Monoclimacis sp.

Plate 3, figs 1–3, 7

Material. Several fragments, the majority of which are distal.

Description. Proximal fragments are gently dorsally curved whilst distal fragments are almost straight. The minimum dorso-ventral width observed is 0.45 mm, the maximum is 0.65 mm. 2TRD values lie between 1.4 mm and 2.0 mm, with the lowest 2TRDs being recorded distally. Distal thecae are of fairly typical monoclimacid appearance, with sharp genicula, and genicular hoods growing out from above simple, slightly everted thecal apertures. Supragenicular walls are, however, gently inclined to the rhabdosome axis. One specimen (UCWG935A, Pl. 3, fig. 2) illustrates the change in thecal morphology from hooked at the first theca preserved, such that the aperture faces proximally, to monoclimacid as seen in the distal thecae. This change takes place rapidly, over four thecae, and involves the retreat of both the dorsal and ventral margins of the hook, so that the former disappears and the latter is modified into the genicular hood.

Remarks. The shape of the rhabdosome and the form of the thecae are very similar to those of *Mcl. crenularis* (Lapworth, 1880), which has only been recorded from the *M. convolutus* Biozone. The latter species reaches a greater width and has more widely spaced thecae, particularly distally, than the present material, from which it may have been derived.

Genus PRISTIOGRAPTUS Jaekel, 1889

Type species. Original designation; *P. frequens* Jaekel, 1889, p. 669, pl. 28, figs 1 and 2; from the Silurian of Germany.

Diagnosis. Thecae simple and straight, or almost straight, throughout length of rhabdosome.

Pristiograptus concinnus (Lapworth, 1876)

Plate 2, fig. 4

- v*1876 *Monograptus concinnus* Lapworth, pp. 320–321, pl. 11, fig. 1.
 v.1911 *Monograptus concinnus* Lapworth; Elles and Wood, pp. 368–369, pl. 36, fig. 5a–e (? f); text-fig. 240.
 1970 *Pristiograptus concinnus* (Lapworth); Rickards, pp. 60–61, pl. 5, fig. 5.
 1975 *Pristiograptus concinnus* (Lapworth); Hutt, pp. 57–58, pl. 12, figs 1, 2, 7, 8.
 1988 *Pristiograptus concinnus* (Lapworth); Štorch, pp. 14–15, pl. 6, figs 2–4; text-fig. 2B.

Lectotype. Designated Přibyl 1948, p. 68; specimen figured Lapworth 1876, pl. 11, fig. 1a, from the Llandovery of Dob's Linn, Moffat, Scotland.

Material. Three fragments.

Description. The fragments are very gently ventrally or dorsally curved, up to 1.2 mm wide with 2TRDs of 2.1–2.2 mm. The thecae are simple tubes, inclined at c. 25° to the rhabdosome axis, with horizontal to sub-horizontal apertural margins, and a slight, often rounded, geniculum at the base of the free ventral wall.

Remarks. The slight geniculum, or convexity of the free ventral wall, of the thecae in this species has been widely illustrated. Hutt (1975) and Rickards, Hutt and Berry (1977) considered this feature to suggest that *Atavograptus atavus* (Jones, 1909) was ancestral to *P. concinnus*.

Genus PRIBYLOGRAPTUS Obut and Sobolevskaya, 1966

Type species. Original designation, Obut and Sobolevskaya 1966, p. 33; *Monograptus incommodus* Törnquist, 1899, p. 11, pl. 2, figs 1–5; from the Llandovery of Sweden.

Diagnosis. (emended herein). Rhabdosome usually long and slender with flexuous curvature, but in one species more robust and straight, and in one with stiff dorsal curvature proximally. Sicula known in only one species, where it is small, reaching to about the aperture of th. 1. Thecae are long, slender, and usually inclined at less than 20° to the axis of the rhabdosome. Thecal apertures usually furnished with lateral lappets (producing 'horns' in pyrite internal moulds), although in one species the distal thecae are of simple pristiograptid form, but with slightly introverted apertures. Thecal apertures usually overhung by a geniculum and, in two species at least, also by a genicular hood.

Remarks. The author recognizes that it is not correct taxonomic procedure to emend a generic diagnosis on a species other than the type species, but feels that emendation is justified in this instance as the internal moulds of the thecae of *Pr. incommodus* and the proximal thecae of *Pr. leptotheca* are so similar.

EXPLANATION OF PLATE 2

- Figs 1 and 3. *Agetograptus* sp., 1, UCWG919D, distal end of rhabdosome; note the sheath-like structure surrounding the nema, $\times 50$. 3, UCWG919D, proximal end; note that the aperture of th1² opens distally to that of th2¹, $\times 40$.
 Fig. 2. *Agetograptus primus* Obut and Sobolevskaya, 1968. UCWG959D, proximal end, $\times 40$.
 Fig. 4. *Pristiograptus concinnus* (Lapworth, 1876), UCWG958A, rhabdosome fragment; note slight genicula, $\times 10$.
 Figs 5–10. *Pribylograptus leptotheca* (Lapworth, 1876). 5, UCWG909C, proximal fragment, $\times 15$. 6, UCWG925B, mesioproximal fragment, $\times 15$. 7, UCWG913A, mesiodistal fragment, $\times 15$. 8, UCWG910A, distal fragment, $\times 15$. 9, UCWG913A, rounded genicular hood of mesiodistal theca, $\times 50$. 10, UCWG909C, proximal theca, $\times 100$.
 All scanning electron micrographs.



LOYDELL, Swedish Llandovery graptolites

Rickards (1976) discussed this genus in detail and included within it *Monograptus incommodus* Tornquist, 1899, *M. argutus* (Lapworth, 1876), *M. leptotheca* Lapworth, 1876, *M. cf. incommodus* sensu Hutt and Rickards 1970, and *M. sandersoni* Lapworth, 1876. The present author is in favour of the retention of those forms with proven or inferred lateral apertural lappets with the genus, i.e. *M. incommodus*, *M. argutus argutus* and *M. leptotheca*, and, in addition, probably *M. cf. incommodus* sensu Hutt and Rickards 1970 and *M. sandersoni*. Until more detailed studies of the thecal apertures of *M. jonesi* Rickards, 1970, *M. argutus sequens* Rickards, 1970, and *M. angustus* Rickards, 1970 are carried out, their assignation of this genus must be, at most, questionable.

Pribylograptus leptotheca (Lapworth, 1876)

Plate 2, figs 5–10; Plate 3, figs 4 and 5

- *.1876 *Monograptus leptotheca* Lapworth, p. 352, pl. 12, fig. 4.
- 1911 *Monograptus leptotheca* Lapworth; Elles and Wood, p. 371, pl. 37, fig. 2; text-fig. 242.
- v.1968 *Monograptus leptotheca* Lapworth; Rickards and Rushton, p. 268, text-figs 2 and 3.
- .1970 *Monograptus leptotheca* Lapworth; Rickards, pp. 68–69, pl. 6, figs 3 and 4; text-fig. 14, fig 37; text-fig. 16, fig. 2.
- ?p1970 *Monograptus* sp. 2; Hutt, Rickards and Skevington, p. 13, pl. 3, figs 58–62 (*non* figs 56 and 57).
- .1975 *Monograptus leptotheca* Lapworth; Bjerreskov, p. 51, pl. 7, figs F and G; text-fig. 16c.
- .1975 *Pribylograptus leptotheca* (Lapworth); Hutt, p. 73, pl. 16, figs 1–3, 7.
- .1988 *Pribylograptus leptotheca* (Lapworth); Štorch, pp. 28–29, pl. 6, fig. 1; text-fig. 2c.

Lectotype. Strachan (1971, p. 57) has noted that the lectotype designated by Přibyl (1948, p. 73), the specimen figured Lapworth 1876, pl. 12, fig. 4a, has not been recognized amongst Lapworth's collection and is probably unrecognizable as a figured specimen.

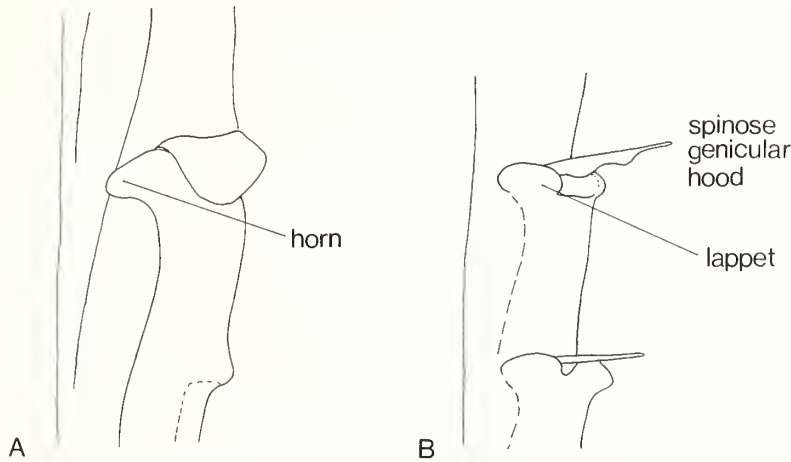
Material. Several hundred proximal, mesial and distal fragments, but possibly belonging to only a few individual rhabdosomes. Most are slightly diagenetically flattened, but some are almost perfectly preserved in three dimensions.

Diagnosis. Rhabdosome more or less straight, of considerable length (probably up to several hundred mm), and with a dorso-ventral width proximally of 0.4 mm increasing gradually to a distal maximum of over 2 mm. Thecae biform; proximally the aperture bears a ventral median saddle together with lateral lappets and is overhung by an angular geniculum furnished with a single-spined genicular hood. Distally the lappets, geniculum and genicular hood retreat until the thecae become simple tubes, although with slight lateral apertural expansion. Overlap of thecae is considerable, increasing from five-eighths proximally to over three-quarters distally. 2TRD is approximately 2.0 mm throughout the rhabdosome. The sicula has not been seen.

Description. The fragments are straight or show slight dorsal curvature. Dorso-ventral width, excluding spines, increases from 0.4 mm proximally to 2 mm distally. Proximal thecae (Pl. 2, figs 5 and 10; Pl. 3, fig. 5) have complex apertures, with a horizontal, median ventral saddle flanked by two distally-directed lateral lappets around which the aperture runs. A broadly triangular genicular hood extending from the angular geniculum of the succeeding theca is furnished with a proximo-ventrally directed spine, 30–40 μ m in diameter and with a length of 0.4 mm. Thecal overlap (determined by embedding a rhabdosome fragment in resin and grinding down with carborundum powder) is five-eighths of the thecal length. Distal thecae (Pl. 2, fig. 8; Pl. 3, fig. 4) are simple tubes, inclined at a low angle to the rhabdosome axis, with slightly introverted and slightly laterally expanded thecal apertures. Distal 2TRD is approximately 2.0 mm, with overlap being greater than three-quarters of the thecal length. Both proximal and distal thecae have a ridge running axially along the middle of the ventral wall of the interthecal septum. This may be a preservational feature. The transition from proximal to distal thecal morphologies takes place gradually in the mesial portion of the rhabdosome (Pl. 2, figs 6, 7, 9) and involves the retreat firstly of the genicular spine and then of the genicular hood, accompanied by the retreat also of the lateral lappets, together with a 'smoothing out' of the geniculum. The sicula has not been seen.

Remarks. Rickards and Rushton (1968) and Bjerreskov (1975) have described well-preserved pyrite internal moulds of this species, but misinterpreted the proximal thecal structure. Their apertural transverse 'horns' and 'hood' are, respectively, a pyrite infilling of the lateral lappets, and of the area between the median saddle and the genicular hood. Text-figure 1 compares the appearance of an internal mould with an isolated specimen. That the genicular spine has not been recognised previously, despite some described specimens (e.g. those of Rickards and Rushton 1968) having some preserved periderm, is surprising. However, as Hutt (1974, p. 35) notes, 'spines may easily be overlooked or inadvertently destroyed when examining specimens preserved in full relief.' The fact that, before examination of the Kallholen fauna, spines had not been recorded on the thecae of *Agetograptus primus*, *Monograptus millepeda* and *M. communis*, the latter two of which are well-known and widely recorded taxa, lends support to Hutt's (1974) observation.

The author agrees with Rickards, Hutt and Berry's (1977) suggested derivation of *Pr. leptotheca* from *Pr. argutus* at the *D. magnus*-*M. argenteus* Biozone boundary.



TEXT-FIG. 1. *Pribylograptus leptotheca* (Lapworth, 1876). A, internal mould of proximal theca (after Rickards and Rushton 1968, fig. 3). B, isolated proximal theca, UCWG926B. Both $\times 25$.

Genus MONOGRAPTUS Geinitz, 1852

Type species. By subsequent designation (Bassler 1915, p. 822): *Lomatoceras priodon* Bronn, 1835, p. 56, pl. 1, fig. 13; from the Silurian of Germany.

Remarks. Detailed discussion of the use and scope of the genus *Monograptus* is to be found in Rickards (1970), Bulman and Rickards (in Bulman 1970) and Bjerreskov (1975).

Monograptus communis communis Lapworth, 1876

Plate 3, figs 6 and 10

- p1876 *Monograptus convolutus* Hisinger, sp. Var. (a.) *communis* Lapworth, p. 358, pl. 13, fig. 4a (non b).
- p1913 *Monograptus communis* (Lapworth); Elles and Wood, pp. 480–481, pl. 49, fig. 1a, c (non b, d, e); text-fig. 336a (non b).
- .1958 *Monograptus communis communis* Lapworth; Sudbury, pp. 520–522, pl. 23, figs 97–101; text-figs 18 and 20.
- 1970 *Monograptus communis communis* Lapworth; Rickards, pp. 84–85, pl. 6, fig. 7; text-fig. 17, figs 1, 19, ?9.
- ?p1982 *Monograptus communis* Lapworth, 1876; Lenz, pp. 67–69, figs 5F, G, T and 21G, H, J, L.

Lectotype. Designated by Elles and Wood 1913, explanation to pl. 49, fig. 1a; specimen figured by Lapworth 1876, pl. 13, fig. 4a, and by Elles and Wood 1913, pl. 49, fig. 1a; BU1684a; from the Lower Birkhill Shales of Dob's Linn, Moffat, Scotland.

Material. Rare fragments, up to c. 5 mm in length.

Description. Proximal fragments are gently dorsally curved, whilst distal ones are almost straight. The thecae are triangular and hooked, with the free ventral wall inclined at c. 20° to the rhabdosome axis. The thecal apertures face proximo-dorsally. They are furnished with a pair of proximo-laterally directed spines up to 0.25 mm long. The maximum dorso-ventral width recorded is 1.15 mm. 2TRD is 1.8–2.15 mm.

Remarks. The thecal apertural spines have not previously been observed, although Sudbury (1958) noted a pair of rudimentary lappets on the lateral parts of the dorsal margins of the thecal apertures on her internal moulds of this species. These lappets represent the infilling of the slight outgrowth of the dorsal thecal apertural margin at the base of each spine.

Lenz (1982) describes (but does not illustrate) uncompressed specimens, which he assigned to *M. communis*, from the Cape Phillips Formation, Cornwallis Island, the metathecal portions of which show strong torsion. These must be specimens of a different species, with *M. denticulatus* Törnquist, 1899, a likely candidate. Both Törnquist (1899) and Bjerreskov (1975) have noted that the apertural regions of the distal thecae of the latter species are twisted laterally, always to the reverse side of the rhabdosome.

Rickards, Hutt and Berry (1977) tentatively suggest that *M. denticulatus* was derived from *M. communis*. The morphological information above would suggest that this is unlikely. However, the discovery of spines on the proximal thecal apertures of *M. millepeda*, described for the first time herein, must strengthen their case for this latter species having been derived from *M. communis*, an evolutionary relationship supported by stratigraphical evidence: *M. communis* appears in the *triangulatus* Biozone whilst *M. millepeda* is first seen in the *argenteus* Biozone to which it is confined.

Storch (1988) has recently identified spines on the thecae of *M. clingani* (Carruthers, 1867) (= *M. communis obtusus* Rickards, 1970) another species which Rickards, Hutt and Berry (*op. cit.*) consider to be derived either from *M. millepeda* or *M. communis*. I would favour derivation from the latter species as overall thecal morphology is more similar. Text-figure 2 illustrates evolution from *M. communis* s.l.

Monograptus denticulatus sensu Sudbury 1958

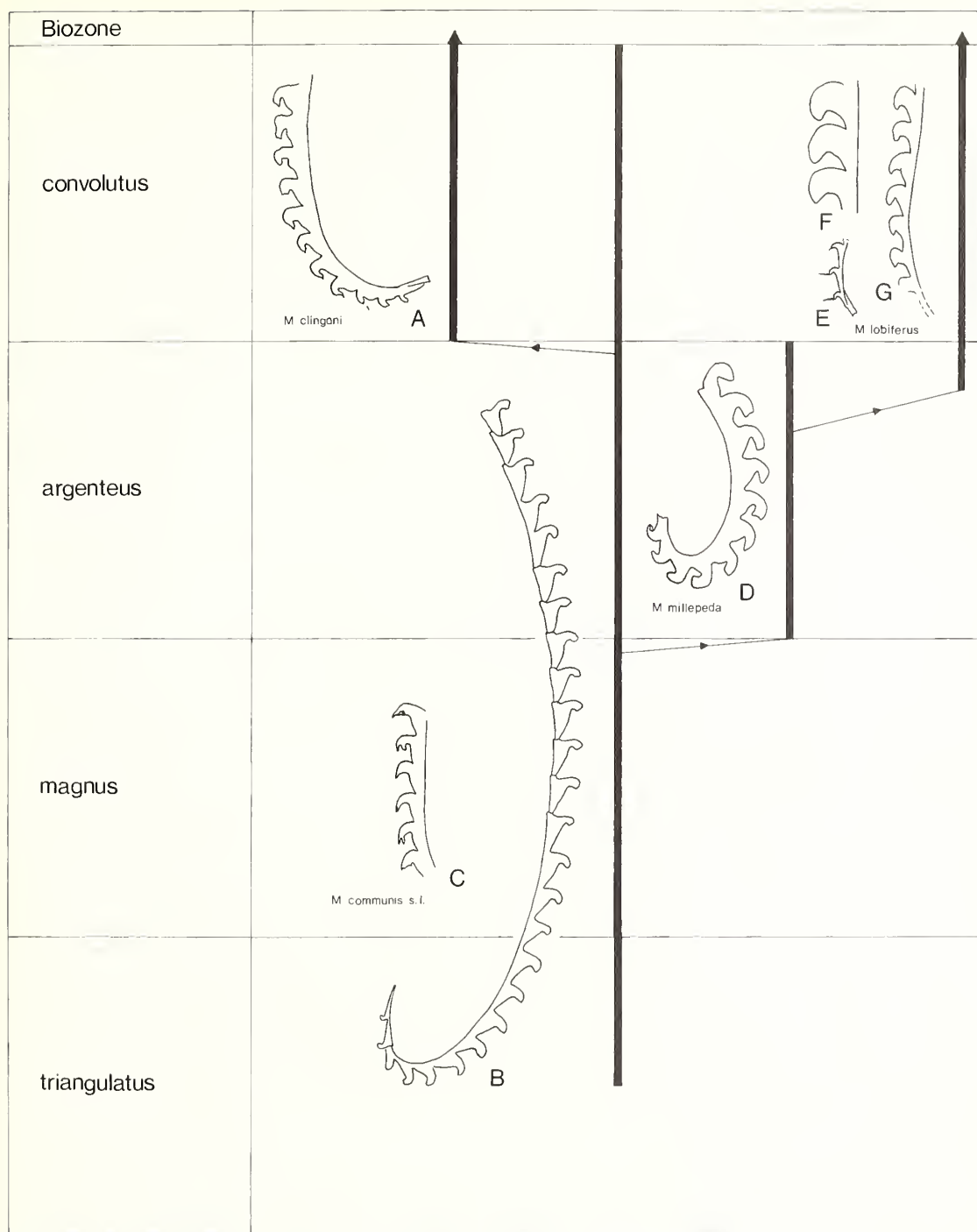
Plate 3, fig. 8

- non 1899 *Monograptus denticulatus* Törnquist, p. 18, pl. 3, figs 19–23.
- 1913 *Monograptus denticulatus* Törnquist; Elles and Wood, pp. 474–475, pl. 48, fig. 2a, b (?c–f); text-fig. 330.
- .1958 *Monograptus denticulatus* Törnquist; Sudbury, pp. 509–510, pl. 21, figs 72 and 73; text-figs 4 and 12.
- 1970 *Monograptus denticulatus* Törnquist; Rickards, pp. 83–84, pl. 7, fig. 3; text-fig. 17, figs 5 and 6.
- non 1975 *Monograptus denticulatus* Törnquist; Bjerreskov, pp. 79–80, text-fig. 23B, c.
- .1975 *Monograptus denticulatus* Törnquist; Hutt, p. 88, pl. 22, fig. 2; pl. 23, figs 1 and 4.

Material. Approximately 50 fragments, though, due to the tenuity of the prothecae, these bear only one or two thecae.

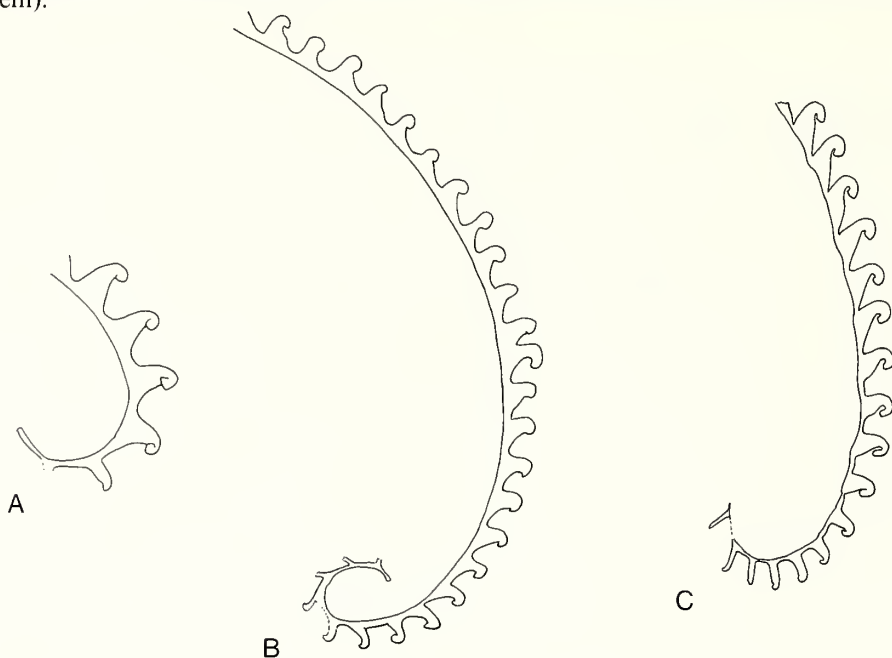
Description. Proximal thecae are rastritiform, whilst distal thecae are more triangular. The protheca is very narrow. Thecal apertures are slightly expanded laterally. They face the dorsal side of the rhabdosome. The maximum dorso-ventral width recorded is 1.25 mm with 1TRD values being 0.95–1.3 mm.

Remarks. The thecal morphology is precisely that interpreted by Sudbury (1958) from slightly compressed material.



TEXT-FIG. 2. Evolution from *Monograptus communis* Lapworth, 1876 s.l. during the Aeronian (= Middle Llandovery). A, *M. clingani* (Carruthers, 1867), after Štorch 1988. B, C, *M. c. communis*; B, after Sudbury 1958; C, UCWG908B. D, *M. millepeda* (M'Coy, 1850), UCWG957A. E–G, *M. lobiferus* (M'Coy, 1850); E, proximal end, after Bjerreskov 1975; F, G, distal and proximal fragments respectively, after Štorch 1988. All $\times 5$.

The thecae of *M. denticulatus* s.s. are less rastritiform proximally, and distally the apertural regions are twisted so as to face the reverse side of the rhabdosome (see Bjerreskov 1975 and Text-fig. 3 herein).



TEXT-FIG. 3. A, B, *Monograptus denticulatus* Törnquist, 1899. A, proximal end, showing twisting of thecal apertures $\times 10$; B, complete rhabdosome, though with damaged proximal metathecae, $\times 5$ (A and B after Bjerreskov 1975). C, *Monograptus denticulatus sensu* Sudbury, 1958, almost complete specimen; note rastritiform proximal thecae, $\times 5$ (after Sudbury 1958).

Clearly, the comments regarding the evolutionary position of *M. denticulatus* given by Sudbury (*op. cit.*) and Rickards, Hutt and Berry (1977) are to the species *sensu* Sudbury, rather than *sensu* Törnquist.

Monograptus millepeda (M'Coy, 1850)

Plate 3, figs 9, 11, 14, 15

- *.1850 *Graptolites millepeda* M'Coy, p. 270.
- .1913 *Monograptus millepeda* (M'Coy); Elles and Wood, pp. 465–466, pl. 46, fig. 10; text-fig. 323.
- .1975 *Monograptus millepeda* (McCoy); Hutt, pp. 96–97, pl. 22, figs 1 and 5; text-fig. 19, fig. 4.
- v.1978 *Oktavites spinatus*, Ni, pp. 411–412, pl. 3, fig. 20; text-fig. 5, figs 1 and 2.
- .1988 *Campograptus millepeda* (McCoy); Storch, pp. 41–42, pl. 9, fig. 2; pl. 10, fig. 4.

Type specimen. Not traced (see Hutt 1975).

Material. Approximately 150 specimens.

Description. The fish-hook shaped rhabdosome bears laterally expanded, triangular, hooked thecae which do not overlap. The hook is retroverted so that the apertures face proximo-dorsally. The proximal thecae each bear a pair of laterally-directed spines, up to 0.3 mm long. These retreat distally, such that by th10 the thecal apertural margin is smooth and non-spinose. Dorso-ventral width at th1 is 0.45–0.5 mm. The maximum width recorded is 1.2 mm. Distal 2TRD is 1.8–2.2 mm. The sicula is 0.9 mm long. Its apex reaches to just above the top of th1.

Remarks. The proximal thecae of *M. millepeda* have not previously been appreciated as being spinose, although Ni (1978) illustrated thecal spines on the conspecific *Oktavites spinatus*.

It is interesting to note that both Pedersen (1922) and Bjerreskov (1975) illustrate paired thecal apertural spines in *M. lobiferus* (M'Coy, 1850). Bjerreskov (*op. cit.*) noted that they were most obvious in the proximal portion of the rhabdosome. It would thus seem likely that *M. lobiferus* evolved from *M. millepeda* by increased retroversion of the thecal aperture and by reduction in rhabdosome curvature (Text-fig. 2). This is at variance with Rickards, Hutt and Berry's (1977) conclusions. They state that there can be little doubt that the lineage *M. sp. A* (*M. sp. 1* of Hutt 1975) (*D. magnus* Biozone) to *M. undulatus* Elles and Wood, 1913 (*M. convolutus* Biozone) led to *M. lobiferus*. The derivation suggested herein, from *M. millepeda*, has a sounder biostratigraphical basis, in that *M. lobiferus* first appears in either the *M. argenteus* or the *M. convolutus* Biozone, whilst, to the author's knowledge, *M. undulatus* has only ever been recorded with certainty from the upper part of the *M. convolutus* Biozone. It should be noted here that Štorch (1988) suggested that the *M. lobiferus* group was derived from *Campograptus* Obut, 1949, a genus into which he placed *M. millepeda*.

Genus RASTRITES Barrande, 1850

Type species. By subsequent designation of Hopkinson 1869, p. 158: *R. peregrinus* Barrande, 1850, p. 67, pl. 4, fig. 6; from the Llandovery of Bohemia.

Diagnosis. Rhabdosome with narrow prothecae and straight, completely isolated metathecae, inclined at a high-angle to the rhabdosome axis. The apertures are hooked and laterally expanded in many species.

Rastrites peregrinus Barrande, 1850

Plate 3, figs 12 and 13

- *.1850 *Rastrites peregrinus* Barrande, p. 67, pl. 4, fig. 6.
- p1914 *Monograptus (Rastrites) peregrinus* (Barrande); Elles and Wood, pp. 488–489, pl. 50, fig. 1a–d (*non e*); text-fig. 343.
- .1941 *Rastrites peregrinus peregrinus* Barrande; Přibyl, pp. 4–6, pl. 1, figs 8 and 9; pl. 2, fig. 8; pl. 3, fig. 13; text-figs 5 and 6.
- 1967 *Rastrites peregrinus peregrinus* Barrande; Schauer, p. 176, pl. 2, figs 5–7.
- .1975 *Rastrites peregrinus peregrinus* Barrande; Bjerreskov, p. 83, pl. 13, fig. A.

Lectotype. Designated Přibyl 1941, p. 3, as the specimen figured by Barrande 1850, pl. 4, fig. 6; from the Llandovery of Bykoš, Bohemia.

Material. Approximately 50 fragmentary specimens.

Description. Parallel-sided metathecae, with a height of up to 2.35 mm, arise from narrow prothecae. They are inclined at 80–90° to the rhabdosome axis. The thecal apertures are slightly hooked so that the crescentic apertures face proximally. 2TRD lies between 2.0 and 2.5 mm. The proximal end has not been seen.

Remarks. This material agrees well with previous descriptions. The thecal apertural region is considerably less hooked than in many other rastritids and this would support Sudbury's (1958) suggested evolution from *M. triangulatus praedecipiens* Sudbury, 1958, although, as Schauer (1967) and Rickards, Hutt and Berry (1977) suggest, this may have been via *R. socialis* Törnquist, 1907.

PALAEOBIOGEOGRAPHICAL NOTE

Melchin (1989) has recently noted close biogeographical affinities between Arctic Canada and Siberia and, to a lesser extent, China from the middle Rhuddanian (= Lower Llandovery) onwards to the top of the Llandovery. Certain genera and species occurring in the above areas are considered to be absent from Europe. These are the genera *Agetograptus*, *Comograptus* Obut and Sobolevskaya, 1968, and '*Paramonoclimacis*' Wang and Ma, 1977 (*Monograptus sidiachenkoi* (Obut and Sobolevskaya, 1965) and *M. falcata* (Chen and Lin, 1978)) and the species and subspecies *Climacograptus janischewskyi* (Obut, 1949), *Metaclimacograptus orientalis* (Obut and Sobolevskaya, 1966), '*Diplograptus*' *tcherskyi* Obut and Sobolevskaya, 1967 spp., *Lagarograptus inexpeditus* Obut and Sobolevskaya, 1968, *Petalograptus ankyratus* NIGP, 1974, *Monograptus* cf. *M. arciformis* Chen and Lin, 1978, and *M. millepeda curtus* (Obut and Sobolevskaya, 1968). This faunal difference is related by Melchin to the ambient current systems.

It is undoubtedly true that a number of the taxa Melchin (1989) quotes appear to exhibit a distribution which is restricted to Arctic Canada, Siberia and China, including, notably, the highly distinctive *M. sidiachenkoi* and *La. inexpeditus*.

However, the records of *Agetograptus prinus* and *Agetograptus* sp. herein (being the first definite records from Europe) necessitate the removal of this genus from Melchin's list of geographically restricted taxa. It should also be noted that Rickards, Hutt and Berry (1977) record *Me. orientalis* from Sweden, and that *M. falcata* may be a junior synonym of *M. argenteus* (Nicholson, 1869), a species widely recorded from Europe.

This is not to say that Melchin's (1989) 'faunal provinces' do not exist, only that the number of geographically restricted taxa involved may be less than he envisages.

Acknowledgements. Special thanks are due to Dr M. G. Bassett who collected the nodules from which the graptolites for this study were isolated and who also provided locality information and to Dr D. E. B. Bates, who initiated the study and assisted with electron microscopy. The research for this work was carried out whilst in tenure of a University of Wales Postgraduate Studentship.

EXPLANATION OF PLATE 3

- Figs 1–3, 7. *Monoclimacis* sp. 1, UCWG935A, distalmost thecae of fragment illustrated in fig. 2, $\times 25$. 2, UCWG935A, fragment showing transition from hooked to monoclimacid thecae, $\times 10$. 3, UCWG935A, fourth theca of fragment illustrated in fig. 2, $\times 50$. 7, UCWG935A, first theca of fragment illustrated in fig. 2, $\times 50$.
- Figs 4 and 5. *Pribylograptus leptotheca* (Lapworth, 1876). 4, UCWG926A, distal thecae, ventral view, $\times 15$. 5, UCWG909C, proximal theca, $\times 50$.
- Figs 6 and 10. *Monograptus communis communis* Lapworth, 1876. 7, UCWG908B, mesial fragment; note thecal spines, $\times 10$. 10, UCWG908B, oblique view of thecal apertures, $\times 35$.
- Fig. 8. *Monograptus denticulatus sensu* Sudbury 1958, UCWG923D, fragment of two thecae, $\times 20$.
- Figs 9, 11, 14, 15. *Monograptus millepeda* (M'Coy, 1850). 9, UCWG957A, distal thecae of specimen illustrated in fig. 15; note absence of thecal spines, $\times 20$. 11, UCWG941A, showing lateral expansion of metatheca, $\times 50$. 14, UCWG941D, view from proximal end; note thecal spines, $\times 30$. 15, UCWG957A, long fragment, but with damaged proximal end, $\times 10$.
- Figs 12 and 13. *Rastrites peregrinus* Barrande, 1850. 12, UCWG924B, rhabdosome fragment with damaged metathecae, $\times 10$. 13, UCWG924A, thecal aperture, $\times 50$.
- All scanning electron micrographs.



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BELEMNITES FROM THE CONIACIAN TO LOWER CAMPANIAN CHALKS OF NORFOLK AND SOUTHERN ENGLAND

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ABSTRACT. Coniacian to Lower Campanian belemnite faunas from the chalks of Norfolk and southern England are described, using univariate and bivariate biometric analyses. The faunas include 13 species, subspecies and groups, referred to the following genera: *Actinocamax* Miller, *Goniotentis* Bayle, *Belemnelloamax* Naidin, and *Belemnitella* d'Orbigny. Two taxa, '*Actinocamax*' *lundgreni* Stolley and *Belemnitella p. propinqua* (Moberg) of the *Belemnitella* lineage, are new for England. The nominate subspecies of *Actinocamax verus* Miller and two other subspecies are discussed. Samples of *Goniotentis* Bayle are compared with samples of *Goniotentis* from NW Germany, Belgium and France, the biostratigraphy of which are well-known. The British specimens of *Belemnelloamax* ex gr. *grossouvrei* (Janet) are listed and reviewed. The concept of *B. praecursor* Stolley is discussed, as well as its relationship to the coeval *B. alpha* Naidin and to *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian. The localities are placed in the international stratigraphic framework on the basis of their belemnite faunas as well as other evidence. The traditional zonation of the Coniacian to Lower Campanian of the British Isles is tentatively correlated with the zonation of NW Germany. The German *Goniotentis* zonation of the upper Coniacian to Lower Campanian is critically assessed. The palaeobiogeography of the Upper Cretaceous belemnites of the North European Province is outlined, and the English Coniacian to Lower Campanian belemnite faunas are commented upon with respect to this framework.

SHARPE (1853) monographed the Upper Cretaceous cephalopods, including the belemnites, of the Chalk of England. In his work he described five belemnite species representing the genera *Neohibolites* Stolley, *Actinocamax* Miller, *Goniotentis* Bayle, and *Belemnitella* d'Orbigny. Almost a century later, Wright and Wright (1951) revised and commented briefly on the species described by Sharpe, as well as on species described by later authors. They listed 13 species which were referred to the following genera: *Neohibolites*, *Actinocamax*, *Goniotentis*, *Belemnocamax* Crick, *Belemnitella*, and *Belemnella* Nowak.

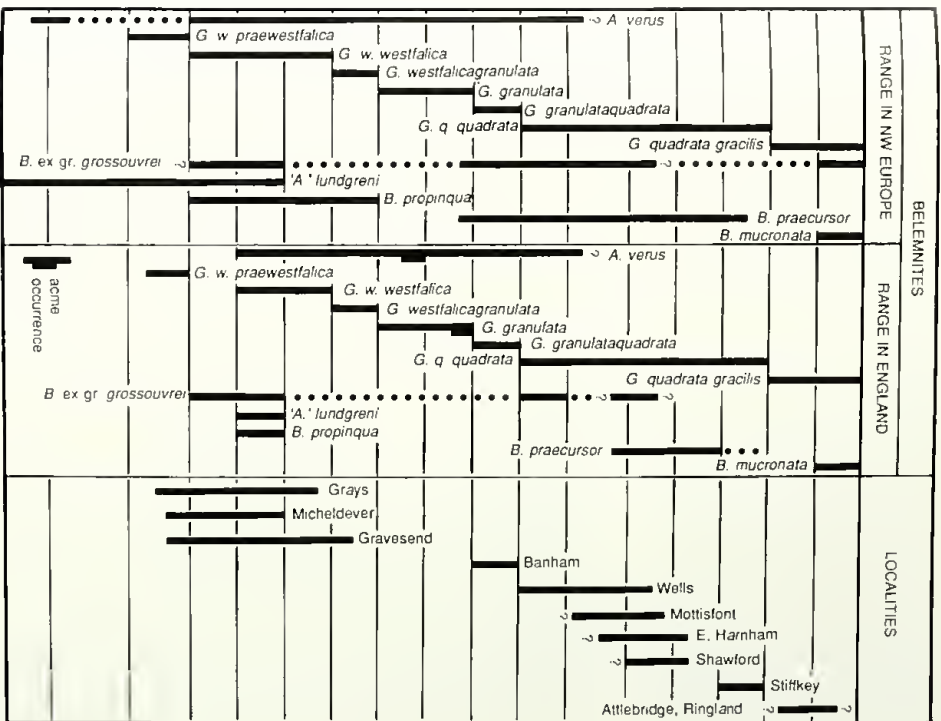
Since 1853 very little systematic palaeontology has been done on the Upper Cretaceous belemnites of Great Britain. This is surprising in view of the large amount of work done on English Lower Cretaceous belemnites and Cretaceous ammonites. As long ago as the 1930s, Brydone (1933, p. 287) stated that: 'Indeed there is hardly any more crying need than that for a thorough study of the belemnites of the Upper Chalk'.

Belemnites are uncommon in the Coniacian to Lower Campanian chalks of England. In the Upper Campanian and Maastrichtian they become more common. The belemnite faunas of the Coniacian to Lower Campanian include species of the *Goniotentis* lineage and *A. verus*, while species of the *Belemnitella* lineage occur sporadically and *Belemnelloamax* is very rare. The Upper Campanian belemnite faunas include only species of *Belemnitella*, and the Maastrichtian faunas comprise species of *Belemnella* with subordinate *Belemnitella*.

The scope of the present paper is to describe the belemnite faunas from the Coniacian–Lower Campanian chalks of Norfolk and southern England, utilizing biometric analysis. Southern England here includes Kent, Essex, Hampshire, and Wiltshire. The uppermost Lower Campanian belemnite fauna from southern England, consisting of *G. quadrata gracilis* (Stolley) and *B. mucronata* (Schlotheim), is not included in the present paper.

STAGE	ZONATION NW GERMANY	TRADITIONAL ZONES		STANDARD BELEMNITE ZONES NW EUROPE
		SOUTHERN ENGLAND	NORFOLK	
LOWER CAMPANIAN	upper part	<i>gracilis</i> / <i>mucronata</i> Zone	post- <i>Applinocrinus</i> beds <i>Applinocrinus</i> <i>cretaceus</i> Subzone <i>Hagenowia</i> <i>blackmorei</i> Horizon	<i>G. quadrata gracilis</i> / <i>B. mucronata</i>
		<i>conica</i> / <i>gracilis</i> Zone		<i>G. quadrata gracilis</i>
		<i>papillosa</i> Zone		<i>G. q. quadrata</i> U
		<i>senonensis</i> Zone		
		<i>pilula</i> / <i>senonensis</i> Zone		
	lower part	<i>pilula</i> Zone	Abundant <i>O. pilula</i> Subzone	<i>G. q. quadrata</i> L
		<i>lingua</i> / <i>quadrata</i> Zone	<i>Echinocorys</i> <i>depressula</i> Subzone	
		<i>granulata</i> - <i>quadrata</i> Zone		<i>G. granulataquadrata</i>
SANTONIAN	U	<i>Marsupites</i> / <i>granulata</i> Zone	<i>Uintacrinus anglicus</i> Zone <i>Marsupites</i> Zone	<i>Marsupites</i> Zone U
		<i>Uintacrinus</i> / <i>granulata</i> Zone	<i>Uintacrinus socialis</i> Zone	<i>Uintacrinus</i> Zone L
	M	<i>rogalae</i> / <i>westfalica</i> - <i>granulata</i> Zone	<i>M. coranguinum</i> Zone	<i>G. westfalica</i> - <i>granulata</i>
		<i>rogalae</i> / <i>westfalica</i> Zone		<i>G. w. westfalica</i> U
		<i>coranguinum</i> / <i>westfalica</i> Zone		<i>G. w. westfalica</i> L
	L	<i>pacti</i> / <i>undulato</i> - <i>plicatus</i> Zone		
	CONIACIAN	<i>bucailli</i> / <i>prae</i> - <i>westfalica</i> Zone		<i>G. westfalica</i> <i>praewestfalica</i>
		<i>involutus</i> / <i>bucailli</i> Zone		
		<i>koeneni</i> Zone		
	L	<i>deformis</i> Zone	<i>M. decipiens</i> Zone <i>M. normanniae</i> Zone	<i>M. cortestudinarium</i> Zone

TEXT-FIG. 1. Zonation and correlation of the Coniacian–Lower Campanian of NW Germany and England, standard belemnite zones in NW Europe, distribution of belemnites in NW Europe and England, and the age of localities according to the present study. The stratigraphical age of the localities is based on belemnites and other evidence.



EARLIER WORK

In addition to Sharpe's monograph (1853), belemnites were described and figured by Miller (1823*a, b*), J. de C. Sowerby (1829), Blackmore (1896), Crick (1906, 1907, 1910), Sherborn (1906), and Brighton (1930). These papers, however, generally are characterized by descriptions of rare species. Jeletzky (1955*a*), in his paper on the evolution of Santonian and Campanian species of *Belemnitella*, also discussed and figured species of *Belemnitella* from the Campanian of England. Christensen (1974) made a morphometric analysis of *Actinocamax plenus* (Blainville) from the Plenus Marls of England, described *A. bohemicus* Stolley from the Middle Coniacian of Yorkshire (Christensen 1982), and discussed *A. primus* Arkhangelsky from England (Christensen 1990).

In addition to the papers mentioned above, English Upper Cretaceous belemnites were discussed, commented upon, and/or used biostratigraphically by Bailey *et al.* (1983*a*, 1984), Ernst (1966), Fletcher and Wood (1978, 1982) Jefferies (1961), Jeletzky (1951*a, b*), Peake and Hancock (1961, 1970), Reid (1971), Rowe (1901, 1904), Schulz (1979), and Wood (1967), to mention the most important papers.

MATERIAL

The belemnite material studied in the present paper was placed at my disposal by the Natural History Museum, London (BMNH), British Geological Survey, Keyworth, Nottingham (BGS), and Sedgwick Museum, Cambridge (SM). It consists of collections made during the last part of the nineteenth century and the beginning of the twentieth century, and includes the collections of H. P. Blackmore, A. W. Rowe, G. E. Dibley, and R. M. Brydone. In addition to these old collections, belemnites collected recently by C. J. Wood, P. Hammond, A. S. Gale and others are also included. The belemnites of the old collections are generally labelled only with locality name and zone. In contrast, the belemnites collected recently are very accurately horizoned with reference to lithological marker beds.

STRATIGRAPHY

The traditional zonation of the Coniacian–Maastrichtian of the British Isles was summarized by Hancock (1972) and Rawson *et al.* (1978) (cf. Text-fig. 1), and later discussed by, among others, Bailey *et al.* (1983*a, b*, 1984), Gale *et al.* (1987), Gale and Woodroff (1981), Mortimore (1986, 1987), Mortimore and Pomerol (1987), Pomerol *et al.* (1987), Robinson (1986, 1987), Stokes (1975, 1977), Wood (1981), and Wood and Mortimore (1988).

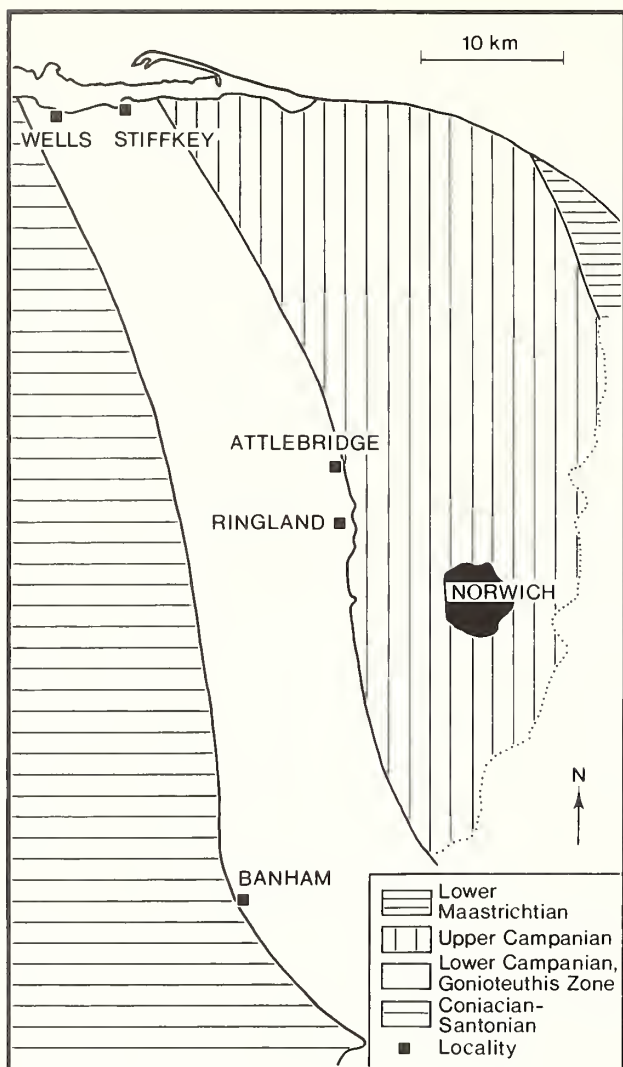
The Lower Campanian of southern England has been subdivided into several units (fossil horizons) (see Peake in Hancock 1972, table I, p. 114; see also Wood and Mortimore 1988); five of these units are shown in Text-figure 1. The Coniacian to Maastrichtian of Norfolk was studied by R. M. Brydone and A. W. Rowe at the beginning of the century; this work was summarized by Peake and Hancock (1961, 1970) and Wood (1988).

The Coniacian–Maastrichtian of NW Germany has been carefully studied during the last twenty-five years by a number of workers (see reviews by Ernst *et al.* 1979; Schulz *et al.* 1984). The zonation applied in Germany is used as a stratigraphic framework in the present paper.

The definition of the Coniacian–Lower Campanian chosen in the present paper is shown in Text-figure 1, and the belemnite zonations of NW Europe, Balto-Scandia, and the Russian Platform are shown in Text-figure 2. The correlation of the zonations in NW Germany and England is tentative and based mainly upon information presented by Bailey *et al.* (1983*a, b*, 1984). The *Uintacrinus socialis* Zone in England is defined by the first occurrence of its index fossil (Bailey *et al.* 1983*a*), whereas in Germany *U. socialis* occurs in both the *Uintacrinus/granulata* Zone and the upper part of the subjacent *westfalicagranulata* Zone (Ulbrich 1971; Ernst and Schulz 1974). The boundary between the Lower and Upper Campanian is placed at the extinction level of the genus *Gonioteuthis*. At the beginning of this century this boundary was placed at a lower level by British workers (e.g. Brydone 1912), namely at the first occurrence of *B. mucronata*. Fletcher and Wood (1978) suggested that the boundary as marked by the extinction level of *Gonioteuthis* was diachronous, being lower in Northern Ireland and England than in Germany.

Belemnite zones, NW Europe		Zonal belemnites, Balto-Scandia		Zonal belemnites, Russian Platform	
U Maastr. U L	<i>B. casimirovensis</i>	U Maastr. U L		U Maastr. U L	<i>B. casimirovensis</i>
	<i>B. junior</i>				<i>B. junior</i>
L Maastrichtian U L	<i>B. fastigata</i>	L Maastrichtian U L		L Maastrichtian U L	<i>B. sumensis</i>
	<i>B. cimbrica</i>				<i>B. lanceolata</i>
	<i>B. sumensis</i>				<i>B. licharewi</i>
	<i>B. obtusa</i>				
	<i>B. pseudobtusa</i>				
	<i>B. lanceolata</i>		<i>B. lanceolata</i>		
Upper Campanian lower part U L	<i>B. 'langei'</i>	Upper Campanian U L		Upper Campanian U L	<i>B. l. najdini</i>
	<i>B. 'minor'</i>				<i>B. l. langei</i>
	<i>B. mucronata</i>		<i>B. mucronata</i>		<i>B. l. minor</i>
Lower Campanian upper part U L	<i>G. q. gracilis</i> / <i>B. mucronata</i>	Lower Campanian U L	<i>B. balsvikensis</i> / <i>B. mucronata</i>	Lower Campanian U L	<i>B. mucronata</i>
	<i>G. q. gracilis</i>		<i>B. mammillatus</i> / <i>G. q. scaniensis</i>		<i>B. mucronata</i> / <i>G. q. gracilis</i> / <i>B. mammillatus</i>
	<i>G. q. quadrata</i>		<i>B. mucronata</i>		<i>B. alpha</i> / <i>B. praecursor</i> / <i>G. q. quadrata</i>
	<i>G. granulataquadrata</i>		<i>G. granulataquadrata</i> / <i>B. alpha</i>		<i>B. praecursor</i> / <i>A. laevigatus</i> / <i>G. granulataquadrata</i> ('Pteria-beds')
Santonian U L	<i>G. granulata</i>	Santonian U L	<i>G. granulata</i>	Santonian U L	<i>B. praecursor</i> / <i>G. granulata</i>
	<i>G. westfalica</i> <i>granulata</i>		<i>G. westfalica</i> <i>granulata</i> / <i>B. propinqua</i>		<i>B. propinqua</i> / <i>A. lundgreni</i> <i>ulicus</i>
	<i>G. w. westfalica</i>		<i>G. w. westfalica</i> / <i>B. propinqua</i> / <i>A. lundgreni</i>		
Coniacian U L	<i>G. westfalica praewestfalica</i>	Coniacian U L	<i>A. lundgreni</i>	Coniacian U L	<i>A. lundgreni</i>
Turonian U L		Turonian U L		Turonian U L	<i>A. plenus triangulus</i>
Cenomanian U L	<i>A. plenus</i>	Cenomanian U L	<i>A. plenus</i>	Cenomanian U L	<i>A. plenus</i>
	<i>A. primus</i>		<i>A. primus</i>		<i>A. primus</i> / <i>N. ultimus</i>

TEXT-FIG. 2. Upper Cretaceous belemnite zones in western Europe, Balto-Scandia, and the Russian Platform (after Christensen 1988).



TEXT-FIG. 3. Map of Norfolk showing Lower Campanian *Gonioteuthis* Zone localities (modified from Peake and Hancock 1970).

LOCALITY DETAILS

The more important localities (Text-figs 3 and 4) mentioned in the text are listed below, with appropriate bibliographical information and National Grid References.

Norfolk (Text-fig. 3)

The chalk pits in the *Gonioteuthis* Zone of Norfolk were discussed by Peake and Hancock (1961, 1970) and Wood (1988).

Wells (TF 928429). According to Peake and Hancock (1970, p. 339A) this pit exposed about 40 m of chalk. The lowest beds were tentatively referred to the upper third of the *depressula* Subzone, the chalk in the middle of the quarry to the *cineta* belt of the Subzone of abundant *O. pilula*, and the top beds to the lowest third of the *H. blackmorei* Horizon.

The belemnites examined during the course of the present study were collected by P. Hammond. The entire section has yielded *Gonioteuthis*, but there is only sufficient material of *Gonioteuthis* for biometrical analysis from the lower third of the section. The specimens from this part of the section are referred to *G. q. quadrata*

and are from the lower part of the *lingua/quadrata* Zone of the lower Lower Campanian. This part of the section also yielded *A. verus*. Moreover, I have seen a single specimen of *Belemnitella* sp., from the *pilula* Zone.

Stiffkey (TF 975428). The chalk pit was placed in the higher part of the *Goniot euthis* Zone by Peake and Hancock (1970, p. 339A). The belemnites examined by me were collected by P. Hammond and include *G. q. quadrata* and *B. cf. praecursor*. The sample of *G. q. quadrata* is regarded to be from the upper Lower Campanian *papillosa* Zone.

Banham (TM 065878?). This is locality no. 129 of Rowe (MS and field notebooks preserved in the Palaeontology Library, BMNH, see Wood 1988). Peake and Hancock (1961, p. 313) recorded '...a typical *Echinocorys tectiformis* Brydone, such as would be expected from the lowest part of the *O. pilula* Zone;'. I have seen five specimens of *G. granulataquadrata* and three specimens of *A. verus* from Banham; the chalk of this pit is thus basal Campanian, *G. granulataquadrata* Zone.

Attlebridge (TG 134165). This is locality no. 168 of Rowe (MS and field notebooks, see Wood 1988). Peake and Hancock (1961) recorded several pits on Alderford Common, 1 mile north of Attlebridge. On the zonal map of Peake and Hancock (plate 1), Attlebridge is placed in the top of the *Goniot euthis* Zone. I have seen a single specimen which may be referred to *G. quadrata gracilis*.

Ringland (TG 13951253). This is possibly locality no. 171 of Rowe (MS and field notebooks, see Wood 1988). According to Wood (1988) the pit is now overgrown and no chalk is visible. The pit was placed very high in the *Goniot euthis* Zone by Wood (1988). I have seen a single specimen, which may be referred to *G. quadrata gracilis*.

Kent and Essex (Text-fig. 4)

Gravesend and Grays. The chalk pits of the Gravesend area, Kent, and the chalk pit at Grays, Essex, were mentioned briefly by Dibley (1900, 1918). He placed them in the top part of the *coranguinum* Zone. Dibley (1900) listed nine pits in the Gravesend area, including Fletcher and Co's Pit. Pits presently available expose chalk of latest Coniacian to Middle Santonian age (A. S. Gale pers. comm. 1985; C. J. Wood pers. comm. 1988).

The chalk pit at Grays has yielded the following belemnites: *G. w. westfalica*, *B. p. propinqua*, and 'A.' ex gr. *lundgreni*. This belemnite fauna is Lower Santonian.

Belemnites from the Gravesend area include *G. w. westfalica*, *G. westfalicagranulata*, *B. p. propinqua*, 'A.' *lundgreni*, *A. verus* and 'A.' ex gr. *lundgreni*; these belemnites are from the upper Lower-Middle Santonian, Zones of *G. westfalica* and *G. westfalicagranulata*.

East Kent. The east Kent succession has yielded *G. westfalica praewestfalica*, *G. w. westfalica*, *G. westfalicagranulata*, *G. granulata*, and *A. verus*; *G. granulata* is common in the *Marsupites* Zone and *A. verus* in the *Uintacrinus* Zone (Bailey *et al.* 1983a).

I have studied three samples of *G. granulata* from east Kent (A. W. Rowe Colln, BMNH) (see below). They are said to come from the *Marsupites* Zone. On the basis of the mean Riedel Quotient, the sample from the Northdown brickworks pit near Margate can be assigned to the Upper Upper Santonian *Marsupites/granulata* Zone. The two samples from Rifle Butts and Margate, respectively, can be referred to the Lower Upper Santonian *Uintacrinus/granulata* Zone. This is at variance with the supposed age given on the labels and the discrepancy may be due to the small number of specimens in the two samples.

Hampshire (Text-fig. 4)

The chalk pits in Hampshire were listed by Griffith and Brydone (1911) and Brydone (1912).

Micheldever. This is locality no. 295 of Brydone (1912), which is a railway cutting north of the station (SU 518434). The cutting exposed chalk of *coranguinum* Zone age. The material in the Blackmore Colln, BMNH probably came from a working pit in the area, exposing chalk of the same age (A. S. Gale pers. comm. 1985). Micheldever has yielded *G. w. westfalica*, 'A.' *lundgreni*, *B. ex gr. grossouvei*, and *A. verus*. Moreover, several specimens of *Goniot euthis*, which are destroyed at the alveolar end and therefore not determinable, are also known from this locality. These belemnites are Lower Santonian.



TEXT-FIG. 4. Map of eastern England showing localities and distribution of the Upper Cretaceous.

Shawford (SU 338274). This is locality no. 1086 of Brydone (1912), also known as Southampton Waterworks New Pit. This pit formerly exposed chalk of the lower *quadrata* Zone, possibly the *H. blackmorei* Horizon according to C. J. Wood (pers. comm. 1983) and A. S. Gale (pers. comm. 1985).

A small sample of *Gonioteuthis* from the 'lower course' sensu Brydone was analysed biometrically and compared with German samples of *Gonioteuthis*. The Shawford sample is referable to *G. q. quadrata* and is regarded to be from the middle Lower Campanian (see below).

I have also studied a small fauna of *Belemnitella* from this pit, mostly specimens without horizon details. The *Belemnitella* fauna is heterogeneous, in contrast to the *Belemnitella* fauna from East Harnham (see below), and includes *B. cf. praecursor* and *B. mucronata*. The *Belemnitella* specimens from the 'lower' or 'bottom course' are all *B. cf. praecursor*. *B. mucronata* appears in the uppermost Lower Campanian *mucronata/gracilis* Zone, and it thus seems that more zones were present at Shawford, spanning the middle to upper Lower Campanian. It is, however, possible that the specimens of *B. mucronata* came from another pit and were purchased from quarry workers.

Mottisfont (SU 337274). Brydone (1912) listed three pits situated north of the Mottisfont Station, locality nos 1065–1067, placed in the *quadrata* Zone. Brydone (1914) discussed locality no. 1067, also referred to as Mottisfont Whiting Pit, and he assigned the lower quarter to the Subzone of abundant *O. pilula*, whereas the upper three-quarters was assigned to the *quadrata* Zone.

Bailey *et al.* (1983a, p. 35) mentioned that the pit exposed chalk of basal *quadrata* Zone age, by and large equivalent to the *H. blackmorei* Horizon. According to Mortimore (1986, fig. 19), however, the pit showed chalks from the Old Nore Marl to above the Pepper Box Marls; the old Nore Marl is low in the Subzone of abundant *O. pilula* and the Pepper Box Marls are high in the *H. blackmorei* Horizon (Mortimore 1986, figs 20 and 22).

I have examined *B. ex gr. grossouvrei* and *A. verus* from Mottisfont. *A. verus* was also recorded by Brydone (1912) in addition to *G. quadrata*. The presence of *A. verus* is enigmatic, because this species is not recorded from above the *depressula* Subzone in southern England (see Bailey *et al.* 1983a, fig. 3; Mortimore 1986, fig. 20). In Germany, *A. verus* ranges up to the top of the *pilula* Zone sensu *germanico* at Misburg/Höver near Hannover (Ernst 1963b). The presence of *A. verus* at Mottisfont may therefore be explained in one of the following ways: (1) *A. verus* has a greater stratigraphic range than assumed by English workers, or (2) older beds may have been exposed formerly at Mottisfont.

Wiltshire (Text-fig. 4)

East Harnham (SU 140288). This pit on the south side of Salisbury is now backfilled, and the collections of Blackmore, now in BMNH, were probably mostly purchased from quarry workers (A. S. Gale pers. comm. 1985). The nearby section at West Harnham currently exposes high *pilula* Zone to basal *quadrata* Zone chalk, and it appears likely that East Harnham exposed approximately the same levels (A. S. Gale pers. comm. 1985).

The belemnites from East Harnham include *G. q. quadrata*, *B. praecursor*, and *B. ex gr. grossouvrei*. The sample of *G. q. quadrata* is regarded to be from the middle Lower Campanian (see discussion below). According to Blackmore (1896), *B. lanceolata* (= *B. praecursor*) occurred in a thin band in the lower third of the *quadrata* Zone. The sample of *B. praecursor* is homogeneous in contrast to the *Belemnitella* fauna from Shawford (see above).

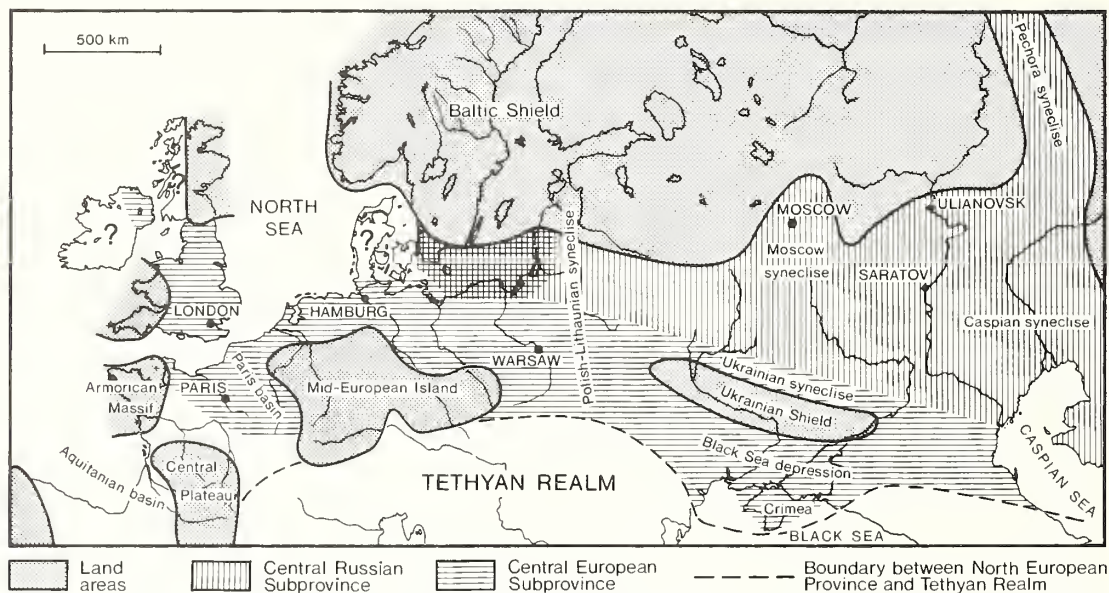
West Harnham. The only belemnite studied by me from this pit is the holotype of *Actinocamax blackmorei* Crick, which is referred to the *B. grossouvrei* group in the present paper. The chalk is presumed to be from the high *pilula* Zone-basal *quadrata* Zone (see above).

PALAEOBIOGEOGRAPHY OF THE UPPER CRETACEOUS BELEMNITES OF NW EUROPE

Christensen (1975a, 1976, 1982) surveyed the palaeobiogeography of the Upper Cretaceous belemnites of Europe (see also Combémere *et al.* 1981), and consequently only a brief outline is given here. Belemnitellidae characterize the North Temperate Realm, but occur also in the northern part of the Tethyan Realm. They are unknown from the southern part of the Tethyan Realm and the South Temperate Realm.

The North Temperate Realm includes the North American and North European Provinces, and

the latter comprises the Central European and Central Russian Subprovinces (Text-fig. 5). The subprovinces are well-defined in the Coniacian–Lower Campanian and characterized by independently evolving belemnite lineages: the *Gonioteuthis* lineage inhabited the Central European Subprovince and the *Belemnitella* lineage (including '*Actinocamax*' *lundgreni*) inhabited the Central Russian Subprovince. *A. verus* and *B. ex gr. grossouvrei* are widely distributed in both subprovinces; *A. verus* occurs commonly, while *B. ex gr. grossouvrei* is very rare (Christensen 1986).



TEXT-FIG. 5. Distribution of Upper Cretaceous biogeographic units in Europe based on belemnites. Upper Cretaceous land and sea areas represent maximum inundation for all stages. The boundaries are not reliable in detail, and the biogeographic units are typically gradational in character. After Christensen (1976).

After the extinction of the genera *Actinocamax* (in the middle Lower Campanian), *Gonioteuthis* (at the Lower–Upper Campanian boundary), and *Belemnelloamax* (in the lower Upper Campanian), the genus *Belemnitella* spread all over the North European Province in the Upper Campanian. The genus *Belemnella* appeared in the basal Maastrichtian and continued to the top of the Maastrichtian. In the Upper Campanian–Maastrichtian, however, no well-defined subprovinces can be recognized.

Norfolk and southern England are situated in the Central European Subprovince as defined by belemnites, but the genus *Gonioteuthis* is generally rarer here than elsewhere.

BELEMNITE FAUNAS OF THE UPPER CONIACIAN–LOWER CAMPANIAN

The late Coniacian chalk of east Kent has yielded a single specimen of *Gonioteuthis westfalica praewestfalica*.

The Lower–Middle Santonian belemnite faunas from Grays, Gravesend, and Micheldever consist of *G. w. westfalica*, *G. westfalica* *granulata*, '*A.*' *lundgreni*, '*A.*' *ex gr. lundgreni*, *B. propinqua*, *A. verus*, and *B. ex gr. grossouvrei*. This diverse fauna includes taxa from both the Central European Subprovince (species of the *Gonioteuthis* lineage) and the Central Russian Subprovince (species of the *Belemnitella* lineage), in addition to the widespread *A. verus* and *B. ex gr. grossouvrei*. The species are very rare with one exception; *A. verus* occurs commonly at Gravesend. '*A.*' *lundgreni* has its main occurrence on the Russian Platform and in Balto-Scandia. Two specimens of '*A.*' *lundgreni* have been recorded earlier as *Gonioteuthis lundgreni*/aff. *westfalica* *sensu* Birkelund (see Ernst

1964a, pl. 3, figs 5 and 6) from the Münster Basin in NW Germany (Christensen 1973). *B. propinqua* has also its main occurrence on the Russian Platform and in Balto-Scania. Outside this area it has only been recorded from southern England (this paper). The specimens of '*A.*' *lundgreni*, '*A.*' ex gr. *lundgreni*, and *B. propinqua* from southern England may be regarded as stray specimens.

The Upper Santonian belemnite fauna consists of *G. granulata* and *A. verus*. According to earlier records, *G. granulata* is common in the *Marsupites* Zone and *A. verus* in the *Uintacrinus socialis* Zone.

The lower to middle Lower Campanian fauna includes *G. granulataquadrata* and *G. quadrata*, with subordinate *B. praecursor*, *B. sp.*, *A. verus*, and *B. ex gr. grossouvrei*. This fauna includes taxa from both of the European subprovinces, as does the Lower to Middle Santonian fauna (see above). The specimens of *B. cf. praecursor* from Shawford, Stiffkey, and Porchester, as well as the specimens of *B. sp.* from Wells and the Sussex coast, may be regarded as stray specimens. *B. praecursor* occurred fairly commonly at East Harnham, and the population consists of all growth stages. This may indicate that *B. praecursor* lived and reproduced in that area during the middle Lower Campanian.

Fletcher and Wood (1978, pp. 93–94) suggested a *B. praecursor* event of considerable biostratigraphic significance in the lower part of the English *quadrata* Zone, by and large equivalent to the *Hagenowia* Horizon (= middle Lower Campanian). They believed that *B. praecursor* occurred at this stratigraphic level in Northern Ireland, Shawford in Hampshire, Bramford and Claydon near Ipswich in Suffolk, Stiffkey in Norfolk, and Hallembaye in eastern Belgium.

In Scania, NW Germany, and Belgium, the genera *Gonioteuthis* and *Belemnitella* occur together in the basal Lower Campanian: *G. granulataquadrata* and *B. alpha* in Scania (Christensen 1975a, 1986), *G. granulataquadrata* and *B. praecursor* at Braunschweig (Ernst 1964b, 1968), *G. quadrata* and *B. alpha*, *B. aff. mucronata/praecursor* or *B. aff. senior/praecursor* in the Münster Basin in NW Germany (Ernst 1964b, Christensen 1986), and *G. quadrata* and *B. praecursor* at Hallembaye in Belgium (Christensen and Schmid 1987). In Scania and NW Germany, the basal Lower Campanian *Gonioteuthis/Belemnitella* assemblage also includes *B. ex gr. grossouvrei* and *A. verus*. As shown above, *B. praecursor* from East Harnham and *B. cf. praecursor* from Shawford are from the middle Lower Campanian, whereas *B. cf. praecursor* from Stiffkey is from the *papillosa* Zone of the upper Lower Campanian. I have briefly studied a sample of *Belemnitella* sp., consisting of more than 100 specimens, from Bramford. This sample was collected by R. M. Brydone and is housed in the Ipswich Museum. On the basis of the external characters only, this sample seems to be more advanced than the samples of *B. praecursor* from Hallembaye and East Harnham, and it may have come from a higher part of the Lower Campanian. In the Corbières area of the French Pyrenees, *B. praecursor* has recently been recorded from the uppermost Santonian (Christensen *et al.* 1991).

It can thus be concluded that there is no evidence for a *Belemnitella praecursor* event in the middle Lower Campanian as suggested by Fletcher and Wood (1978), even if *B. praecursor* is recorded from the middle Lower Campanian of Northern Ireland and southern England.

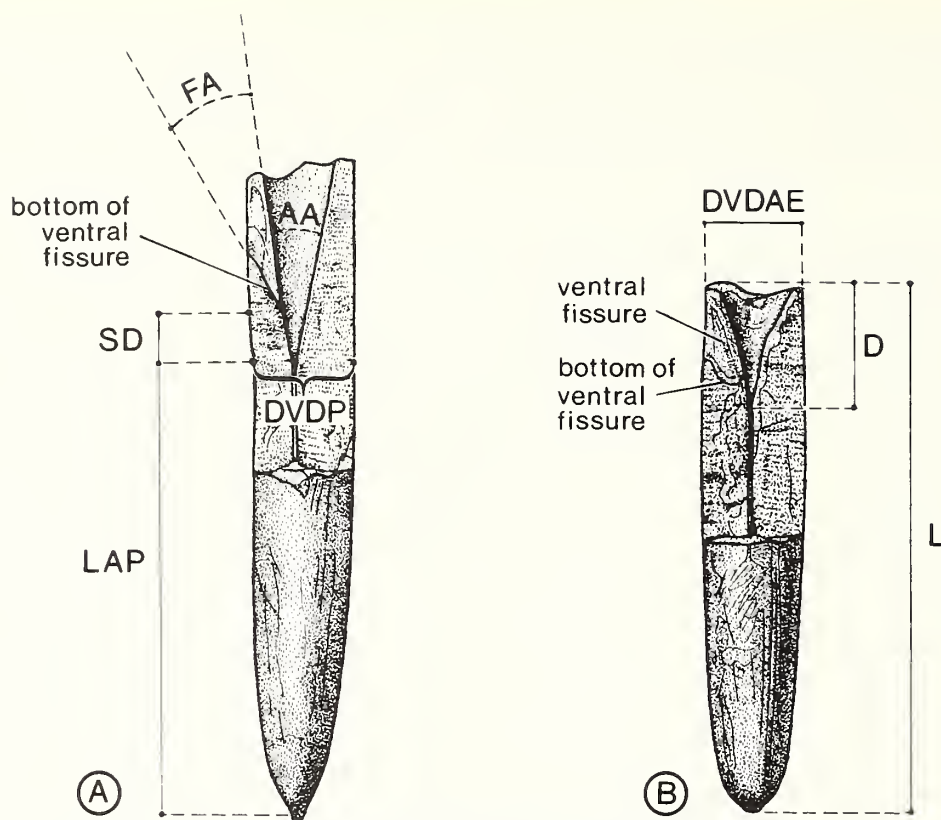
SYSTEMATIC PALAEOONTOLOGY

Morphology of the guard and terminology. The guard is usually the only part of the skeleton preserved, and both external and internal characters are used for taxonomic classification.

The following characters are generally considered to be of taxonomic value in describing Upper Cretaceous belemnites belonging to the Belemnitellidae Pavlow: (1) size of guard; (2) shape of guard; (3) structure of the anterior end; (4) surface markings; (5) internal characters; and (6) ontogeny. The characters were discussed recently by Christensen (1986).

The Riedel Quotient (Ernst 1964a) is the ratio of length of guard divided by depth of pseudoalveolus, and the Schlankheits Quotient (= Slenderness Quotient) of Ernst (1964a) is the ratio of length of guard divided by dorso-ventral diameter at the anterior end.

Measurements and abbreviations. A list of measured characters and abbreviations is given below (cf. Text-fig. 6): total length of guard (L), length from apex to protoconch (LAP), dorso-ventral diameter at protoconch



TEXT-FIG. 6. Diagram showing the morphological elements of the guard in (A) *Belenmitella praecursor* and (B) *Gonioteuthis quadrata*. L = length of the guard; LAP = length from the apex to the protoconch; D = depth of the pseudoalveolus; SD = Schatzky distance; DVDP = dorso-ventral diameter at the protoconch; DVDAE = dorso-ventral diameter at the alveolar end; FA = fissure angle; and AA = alveolar angle. After Christensen and Schmid (1987).

(DVDP), lateral diameter at protoconch (LP), dorso-ventral diameter at alveolar end (DVDAE), lateral diameter at alveolar end (LDAE), maximum lateral diameter (MLD), Schatzky distance (SD), alveolar angle (AA), fissure angle (FA), Riedel Quotient (RQ), and Slenderness Quotient (SQ).

Linear measurements were made with a vernier caliper to an accuracy of 0.1 mm, and angles were measured with a goniometer ocular fitted on a WILD stereomicroscope to an accuracy of 0.5°.

Biometric methods. Species and subspecies variability is analysed using univariate and bivariate statistical methods and is summarized by descriptive statistics, histograms, and scatter diagrams. The statistics were calculated according to standard formulae presented by Simpson *et al.* (1960) and Sokal and Rohlf (1969). The statistical methods and tests used in the present paper were discussed at length by Christensen (1975a, pp. 31–33).

In the univariate analyses estimates of the following statistics were calculated: arithmetical mean value ($\bar{X}$), standard deviation (SD), and coefficient of variation (CV). In addition, observed range (OR) is reported, and N is the number of specimens.

The regression line is written: $y = a + bx$, and the original measurements were used in the calculations, because of the linear trend on ordinary graph paper and the homoscedastic variance around the regression line. Estimates of the following statistical parameters were calculated: the slope (b) and standard deviation of the slope (SD_b); the intercept on the y -axis (a) and the standard deviation of the intercept (SD_a); the variance (SD_{yx}^2) and the standard deviation (SD_{yx}) of the regression line; and the correlation coefficient (r). N is the number of

specimens. The correlation coefficients were tested for significance by using table Y in Rohlf and Sokal (1969), and *t*-tests on the *y*-intercepts were performed in order to see if the intercept differed significantly from zero. The regression lines of two samples were compared in the way described by Hald (1957, pp. 571–579).

I have earlier discussed the disadvantages of using ratios in palaeontological studies (Christensen 1973, 1974, 1975a, 1988) especially in cases where growth is allometric. In the present paper, various ratios were calculated only in order to facilitate comparison with samples of belemnites described by earlier authors.

Order BELEMNITIDA Zittel, 1895
Suborder BELEMNOPSEINA Jeletzky, 1965
Family BELEMNITELLIDAE Pavlow, 1914

Type genus. *Belemnitella* d'Orbigny, 1840.

Diagnosis. See Christensen (1975a).

Distribution. Belemnitellidae are restricted to the Upper Cretaceous and are reported from the Lower Cenomanian to the Upper Maastrichtian. They are mainly distributed in the North Temperate Realm. A few representatives are also recorded from the northern part of the Tethyan Realm.

Genus ACTINOCAMAX Miller, 1823

Type species. *Actinocamax verus* Miller, 1823 by original designation.

Remarks. Naidin (1964) recognized three subgenera within *Actinocamax*: *A.* (*Actinocamax*), type species *A. verus* Miller, 1823; *A.* (*Praeactinocamax*), type species *A. plenus* (Blainville, 1825); and *A.* (*Paractinocamax*), type species *A. grossouvrei* Janet, 1891. This classification was discussed by Christensen (1982, 1986) and is not followed here. Species belonging to *A.* (*Actinocamax*) and *A.* (*Praeactinocamax*) differ only in size, and species referred to *A.* (*Paractinocamax*) by Naidin are placed in the genus *Belemnelloamax* Naidin (see discussion below).

Distribution. *Actinocamax* ranges from the Lower Cenomanian to the middle Lower Campanian. It is distributed in the North European and North American Provinces.

Actinocamax verus Miller, 1823

Plate 1, figs 1–9

- 1823b *Actinocamax verus* Miller, p. 64, pl. 9, figs 17 and 18 (non pl. 3, figs 16–20).
- 1906 *Actinocamax verus* Miller; Sherborn, p. 152, pl. 15, figs 4 and 5.
- 1952 *Actinocamax verus* var. *diestrensis* Naidin, p. 66, pl. 1, fig. 9; pl. 2, figs 1 and 2.
- 1962 *Actinocamax verus diestrensis* Naidin; Kongiel, p. 113, pl. 20, figs 14–17.
- 1964 *Actinocamax* (*Actinocamax*) *verus verus* Miller; Naidin, p. 28, text-figs 9 and 10, 18.
- 1964 *Actinocamax* (*Actinocamax*) *verus diestrensis* Naidin; Naidin, p. 29.

Type. Lectotype, here designated, the original of Miller (1823b, pl. 9, figs 17 and 18).

Material. More than two hundred specimens in the BMNH, BGS, and SM collections: about one hundred specimens from the *coranguinum* Zone of Gravesend, Kent (e.g. Red Lion Pit and Fletcher's Pit) and Micheldever, Hampshire (including BMNH C42708–99 and SM B836–9 from Gravesend, BMNH C43367–77, C44167 and SM B100082–3 from Micheldever); about one hundred specimens from the *Uintacrinus socialis* Zone of southern England (including BMNH C43393–486, SM B65905–19, BGS Zt848); and about one dozen specimens from the *pilula* and *quadrata* Zones of southern England and the *Gonioteuthis* Zone of Norfolk (including BMNH C43357–8, BMNH C44876, BMNH C43359–61, BGS GSM 101426).

Description. An *Actinocamax* with a small, stout guard which is lanceolate in lateral and ventral views. The

guard is flattened ventrally and the anterior end is compressed. The anterior end may have a low or high cone-shaped alveolar fracture, be flat, or even have a shallow pseudoalveolus. There is a small pit in the anterior end for housing the posterior part of the phragmocone. The alveolar fracture is symmetric or asymmetric, and in the latter case the dorsal side is more incised than the ventral side. The alveolar fracture may be sharply demarcated from the surface of the guard or may continue gradually into the surface of the guard. The anterior end exhibits concentric growth layers of the guard and radiating ribs. Dorso-lateral longitudinal depressions are faintly developed, and the vascular imprints are weakly developed or not present. The ventral fissure and ventral furrow are not preserved. The surface of the guard may be covered by granules which may form corrugated transverse lines.

Remarks. *A. verus* can be distinguished easily from other species of *Actinocamax* by its small size and stout guard. Specimens of *A. verus* having a flat anterior end or a shallow pseudoalveolus differ from juvenile specimens of *G. westfalica* in being stouter and more lanceolate in ventral view. Naidin (1964) recognized three subspecies of *A. verus*: *A. v. verus*, *A. verus fragilis* Arkhangelsky, and *A. verus dneptrensis* Naidin, mainly on the basis of the structure of the anterior end. The subspecies were discussed by Christensen (1986), who placed *A. verus dneptrensis* in synonymy with *A. v. verus*, and suggested that *A. verus fragilis* may be considered as a geographic subspecies prevailing on the Russian Platform.

Two samples of *A. verus*, one from the Red Lion Pit, Gravesend (basal Santonian) (BMNH C42708–99), and another from Margate, Kent (Lower Upper Santonian) (BMNH C43393–486), were analysed with respect to the structure of the anterior end (Table 1). In addition, the analysis of two samples of *A. verus* from Scania, Sweden is also reported (Christensen 1986).

All samples showed a series of forms ranging from specimens with a high cone-shaped alveolar fracture (*fragilis*-like specimens), through specimens with a low cone-shaped alveolar fracture (*verus*-like specimens), to specimens with a shallow pseudoalveolus (*dneptrensis*-like specimens), with all intermediate forms. The specimens of the four samples, nevertheless, were subdivided into three groups, although it was difficult in some cases to decide to which group an individual specimen should be assigned. Most specimens in all four samples belong to group 1 (Table 1). A few specimens belong to groups 2 and 3. In the opinion of the author the samples exhibit a normal variation with respect to the structure of the anterior end; similar variations are also seen in other

EXPLANATION OF PLATE 1

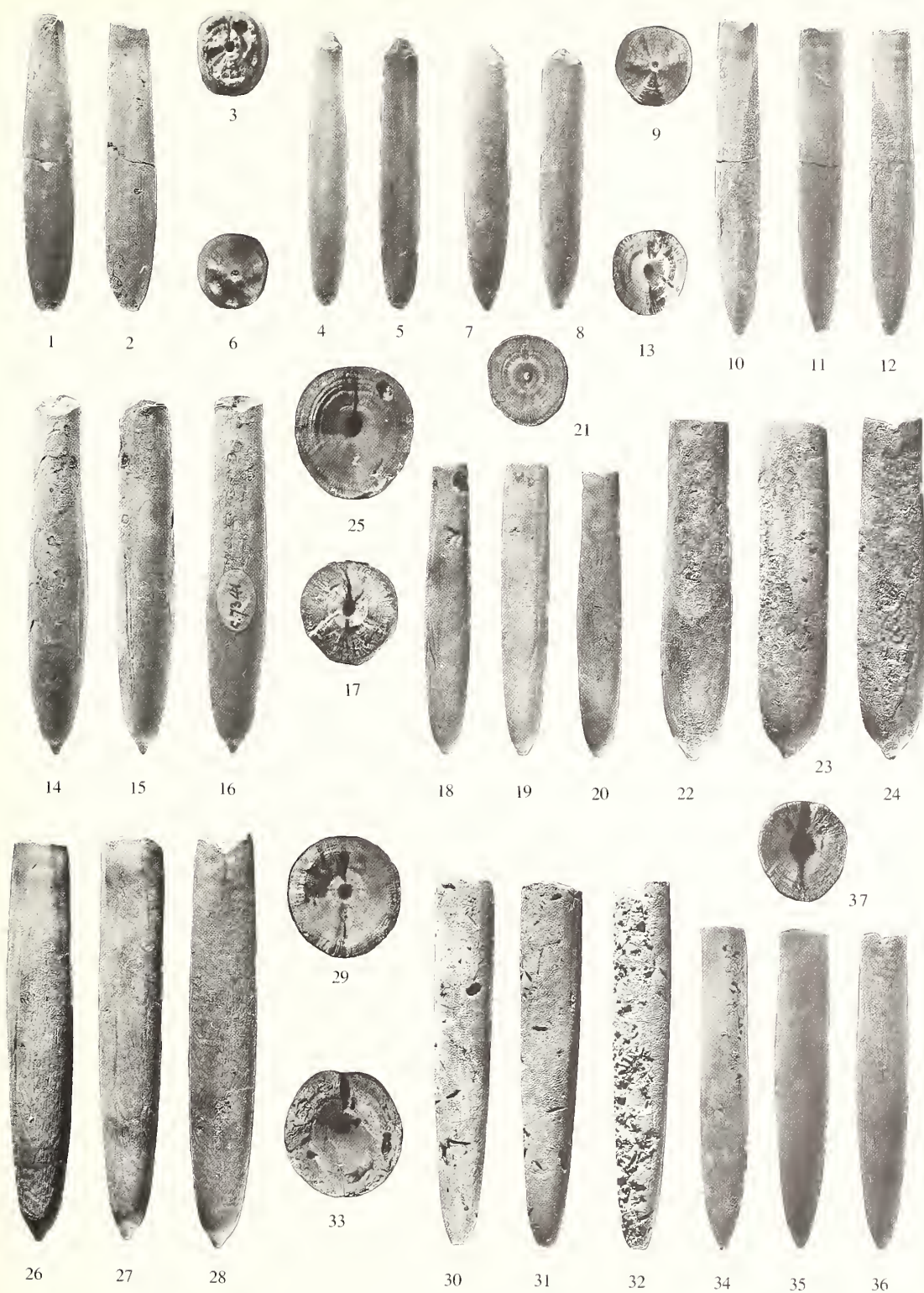
Figs 1–9. *Actinocamax verus* Miller. 1–3, BGS GSM 101427, great cutting north of Micheldever, locality 295 of Brydone (1912), *coranguinum* Zone; 1, dorsal view; 2, lateral view; 3, view of the anterior end, $\times 2$. 4–6, BGS GSM 101426, Mottisfont, locality 1067 of Brydone (1912), *quadrata* Zone; 4, dorsal view; 5, lateral view; 6, view of the anterior end, $\times 2$. 7–9, BGS Zt848, Grenham Bay, Birchington, Kent; uppermost 2 m of *U. socialis* Zone. 7, dorsal view; 8, lateral view; 9, view of anterior end, $\times 2$.

Figs 10–13. *Goniotentis westfalica praewestfalica* Ernst and Schulz, BGS GSM 118339, West Cliff, Ramsgate, Kent; *coranguinum* Zone, 10.0–10.5 m beneath Bedwell's Columnar Band; 10, dorsal view; 11, lateral view; 12, ventral view; 13, view of the anterior end, $\times 2$.

Figs 14–29. *Goniotentis westfalica westfalica* (Schlüter). 14–17, BMNH C7341, Grays, Essex, *coranguinum* Zone; 14, dorsal view; 15, lateral view; 16, ventral view; 17, view of the anterior end, $\times 2$. 18–21, BMNH C44381, Micheldever, *coranguinum* Zone; 18, dorsal view; 19, lateral view; 20, ventral view; 21, view of the anterior end, $\times 2$. 22–25, BMNH C43497, Gravesend, *coranguinum* Zone; a short and stout specimen; 22, dorsal view; 23, lateral view; 24, ventral view; 25, view of the anterior end, $\times 2$. 26–29, BMNH C43496, Gravesend, *coranguinum* Zone; 26, dorsal view; 27, lateral view; 28, ventral view; 29, view of the anterior end, $\times 2$.

Figs 30–37. *Goniotentis westfalica granulata* (Stolley). 30–33, BMNH C43521, Gravesend, *coranguinum* Zone; 30, dorsal view; 31, lateral view; 32, ventral view; 33, view of the anterior end, $\times 2$. 34–37, BGS Zt1960, White Ness near Kingsgate, Kent, *coranguinum* Zone, 1 m above Barrois Sponge Bed; 34, dorsal view; 35, lateral view; 36, ventral view; 37, view of the anterior end, $\times 2$.

All specimens are coated with ammonium chloride and the figures are natural size unless otherwise stated.



samples of *Actinocamax*, i.a. *A. plenius* (see Christensen 1974), and in *G. westfalica* (see Ernst 1964a; Christensen 1975a). It should, however, be stressed that there is apparently an increase in the number of *fragilis*-like specimens from the basal Santonian to the basal Campanian. Ernst (1964b, p. 181) has also reported that *fragilis*-like specimens are more common in the basal Campanian than in the basal Santonian. This apparent trend in the development of the structure of the anterior end may be real, but should be tested by further studies.

Locality	Age	Group 1	Group 2	Group 3	Σ
Kullemölla, Scania	basal Campanian	122 (79%)	26 (17%)	6 (4%)	154
Margate, Kent	Lower Upper Santonian	61 (77%)	16 (20%)	2 (3%)	79
Eriksdal, Scania	upper Middle Santonian	100 (86%)	9 (8%)	7 (6%)	116
Red Lion Pit, Gravesend	basal Santonian	80 (94%)	1 (1%)	4 (5%)	85

TABLE 1. Estimates of relative abundance of three groups of *Actinocamax verus*. Group 1 contains specimens with a low cone-shaped alveolar fracture (*verus*-like specimens); group 2 includes specimens with a high cone-shaped alveolar fracture (*fragilis*-like specimens); and group 3 contains specimens with a shallow pseudoalveolus (*dnestrensis*-like specimens).

Distribution. *A. verus* is widespread in the North European Province. In NW Europe it is recorded mainly from the uppermost part of the Lower Santonian *I. undulatopectatus* Zone to the middle Lower Campanian *Offaster pilula* Zone *sensu germanico*. In off-shore chalks *A. verus* is most common in the Upper Santonian. *A. verus* is also known from the Lower to Middle Coniacian of Bornholm, Denmark (personal observation). On the Russian Platform it occurs in the Turonian to lower Lower Campanian (Naidin 1964).

Genus GONIOTEUTHIS Bayle, 1878

Type species. *Belemnites quadratus* Blainville, 1827 by original designation.

Remarks. The evolutionary lineage of *Gonioteuthis* (in ascending order): *G. westfalica praewestfalica* Ernst and Schulz, *G. w. westfalica* (Schlüter), *G. westfalicagranulata* (Stolley), *G. granulata* (Blainville), *G. granulataquadrata* (Stolley), *G. quadrata quadrata* (Blainville), and *G. quadrata gracilis* (Stolley), has been studied especially by Stolley (1897, 1916, 1930), Ernst (1963a, b, 1964a, b, 1966, 1968), Ernst and Schulz (1974), Christensen (1975a, b, 1986, 1988), Christensen and Schmid (1987), and Jarvis (1980).

Naidin (1964) recognized two subgenera of *Gonioteuthis*: *G. (Gonioteuthis)*, type species *Gonioteuthis quadrata* (Blainville); and *G. (Goniocamax)* Naidin, type species *Actinocamax lundgreni* Stolley. The subgenera were treated later as genera by, among others, Naidin and Kopaevich (1977) and Naidin (1981). Naidin (1964) placed the earliest members of the *Gonioteuthis* lineage in the subgenus *Goniocamax*, in addition to '*Actinocamax*' *lundgreni* Stolley, and other species from the Russian Platform, Greenland, and North America. The classification of Naidin was discussed by Ernst and Schulz (1974) and Christensen (1982, 1986) and is not followed here. '*A.*' *lundgreni* and *G. (Goniocamax)* are discussed further below.

The *Gonioteuthis* lineage provides a good tool for biostratigraphy. It is, however, necessary to analyse homogeneous samples of a certain size in order to make a reliable specific determination, and limited material has little stratigraphic value (Ernst 1964a; Christensen 1975a) (see also below). Only the earliest member of the lineage, *G. westfalica*, is easily recognizable owing to its structure of the anterior end.

Ernst (1963a, b, 1964a, b, 1966, 1968) and Ernst and Schulz (1974) characterized samples of *Gonioteuthis* on the basis of the mean values of various ratios, including the Riedel Quotient and the Slenderness Quotient (Schlankheits Quotient of Ernst).

In order to analyse the growth relationship of various characters, I have calculated regression lines by the least squares method of samples of *Gonioteuthis* from NW Germany on the basis of Ernst's original measurements, which he kindly placed at my disposal. In addition, samples from Sweden, Bornholm (Denmark), Belgium, France, and England have also been analysed (Christensen 1971, 1973, 1975a, b, 1986, herein; Christensen and Schmid 1987).

1. *Length of guard vs depth of pseudoalveolus*. 24 samples of *Gonioteuthis* were analysed, including 3 samples of *G. westfalica* from NW Germany and Bornholm, 3 samples of *G. westfalicagranulata* from NW Germany and Sweden, 1 sample of *G. granulata* from NW Germany, 1 sample of *G. granulataquadrata* from NW Germany, 13 samples of *G. q. quadrata* from different levels within the Lower Campanian of NW Germany, Belgium, France, and England, 2 samples of *G. quadrata gracilis* from the top Lower Campanian of NW Germany, and 1 sample of *G. quadrata scaniensis* Christensen from the top Lower Campanian of Sweden.

An isometric relationship of the two variates was found in 21 samples. The three samples showing an allometric relationship are *G. quadrata gracilis* from the *conica/gracilis* and *gracilis/mucronata* Zones of Misburg/Höver in NW Germany, respectively, in addition to *G. q. quadrata* from the lower *lingua/quadrata* Zone of the C.P.L. Quarry at Hallembaye in Belgium. In *G. quadrata gracilis* from the *gracilis/mucronata* Zone the growth relationship is strongly allometric, while in *G. quadrata gracilis* from the *conica/gracilis* Zone and *G. q. quadrata* from Hallembaye it is slightly allometric.

2. *Length of guard vs dorso-ventral diameter at the alveolar end*. 19 samples were analysed: 3 samples of *G. westfalica*, 1 sample of *G. westfalicagranulata*, 1 sample of *G. granulataquadrata*, 11 samples of *G. q. quadrata*, 2 samples of *G. quadrata gracilis*, and 1 sample of *G. quadrata scaniensis*.

An allometric relationship was found in 12 samples. The seven samples showing an isometric relationship are *G. granulataquadrata* from Weinberg, *G. q. quadrata* from the lower *lingua/quadrata* Zone of Höver and Hallembaye, *G. q. quadrata* from the lower *senonensis* Zone of Höver, in addition to three samples from England and France: Shawford, 'lower course' (middle Lower Campanian); Stiffkey (*papillosa* Zone); and Hardivillers (middle Lower Campanian).

In my opinion, samples of *Gonioteuthis* are better characterized by statistical parameters of the regression analyses than by ratios. Ernst's *Gonioteuthis* zonation based on the mean Riedel Quotient is valid, however, because the relationship of length of guard vs depth of pseudoalveolus is isometric in almost all analysed samples of *Gonioteuthis*. The *Gonioteuthis* zonation is discussed further below.

In the analyses of length of guard vs dorso-ventral diameter at the alveolar end, the relationship is allometric to strongly allometric in most samples. It is therefore not valid to calculate the mean Slenderness Quotient.

According to Ernst (1964a, fig. 12), samples of *G. q. quadrata* and *G. quadrata gracilis* from the upper *senonensis* Zone and above are characterized by having a mean Slenderness Quotient of 6.0 or more, with the mean value increasing stratigraphically upwards. The increasing mean value of the Slenderness Quotient, however, is a function of the allometric relationship of length of guard vs dorso-ventral diameter in connection with the diminishing mean length of the guard in samples of *Gonioteuthis* from the upper Lower Campanian. Due to the allometric relationship, small guards are generally more slender than large guards, and consequently the mean Slenderness Quotient will increase when the mean length of the guard decreases.

Phylogeny of Gonioteuthis. The *Gonioteuthis* lineage is an outstanding example of phyletic gradualism, namely slow gradual transformation of a suite of characters within populations through time. The *Gonioteuthis* stock existed for about 10 Ma and the general trend in evolution is the gradual calcification of the anterior part of the guard. In *G. westfalica* the anterior end may be convexly conical, flat, or developed as a shallow pseudoalveolus, while in stratigraphically younger representatives the depth of the pseudoalveolus increases and may be up to one-third of the entire length of the guard. Simultaneously with the development of a deeper pseudoalveolus, the guard

becomes increasingly stout and large, reaching a maximum in *G. quadrata*. Another characteristic feature is the gradual development of granulation. The oldest member, *G. westfalica praewestfalica*, does not possess granulation (Ernst and Schulz 1974). The succeeding taxon, *G. w. westfalica*, shows a wide variation with respect to this character; some specimens carry scattered granules on the dorsal and/or ventral side of the guard, while in others the granules appear to be arranged in longitudinal rows. The same pattern is also valid for *G. westfalicagranulata*. In stratigraphically younger species, however, the granulation becomes a very prominent character. In samples of *G. westfalica* the shape of the guard is highly variable, and a great proportion of the guards are lanceolate in ventral view. In younger populations the variation in the shape of the guard is smaller, and guards which are lanceolate in ventral view are relatively rare. The cross-section of the anterior end is oval to pointed oval in *G. westfalica* and subrectangular to subquadrate in stratigraphically younger representatives, with all intermediate stages. In the uppermost Lower Campanian, the genus *Gonioteuthis* is characterized by a return of earlier features; e.g. reduced length of the guard, diminished depth of the pseudoalveolus, and increased slenderness of the guard.

STAGES	ZONATION NW-GERMANY (1)	GONIOTEUTHIS ZONES (2)	SAMPLES OF GONIOTEUTHIS				
			(3) LAGER- DORF	(4) MISBURG /HOVER	(5) OTHER AREAS	(6) RIEDEL- QUOTIENT 20 18 16 14 12 10 8 6 4 2	
LOWER CAMPA- NIAN	gracilis /mucronata Zone	G. quadrata gracilis (RQ = $\pm$ 4.5) (RQ = 4.0-4.5)		RQ = 4.5			
	conica/gracilis Zone		RQ = 4.7 RQ = 4.5 RQ = 4.2	RQ = 4.5			
	papillosa Zone		RQ = 4.2 RQ = 3.8 RQ = 3.8 RQ = 3.9 RQ = 4.0	RQ = 4.1			
	senonensis Zone	G. quadrata quadrata (RQ = $\pm$ 4.0)	RQ = 3.9 RQ = 4.0 RQ = 3.9 RQ = 4.5	RQ = 3.7			
	pilula/senonensis Zone		RQ = 4.2 RQ = 4.2	RQ = 3.8			
	pilula Zone		RQ = 4.2 RQ = 4.1	RQ = 3.9			
	lingua/quadrata Zone		(RQ = 4.0-5.0) RQ = 3.9	RQ = 4.0 RQ = 4.3 RQ = 4.9			
	granulataquadrata Zone	G. granulata- quadrata (RQ = 5.0-6.0)	RQ = 5.5			RQ = 5.1	
	SANTONIAN	Marsupites/granulata Zone	G. granulata (RQ = 6.0-7.0) (RQ = 7.0-8.0)	RQ = 6.5			
		Untacrinus/granulata Zone		RQ = 6.9 RQ = 8.1			
westfalicagranulata Zone		G. westfalica- granulata (RQ = 8.0-9.5)	RQ = 8.8	RQ = 9.0			
cordiformis/westfalica Zone		G. westfalica westfalica (RQ = 9.5-11.5) (RQ = > 11.5)	RQ = 11.0 RQ = 13.0	RQ = 10.0			
CONIACIAN	undulatoaplicatus Zone						
	praewestfalica Zone	G. westfalica praewestfalica	RQ = 13.0				
	involutus Zone						
	koeneni Zone						
	deformis Zone						

TEXT-FIG. 7. Zonation of the Coniacian-Lower Campanian of NW Germany, *Gonioteuthis* zones, and the mean value and observed range of the Riedel Quotient. Column 2 shows the mean value of the Riedel Quotient of typical samples, column 3 the mean value of small, closely-spaced, samples from the chalk of Lägerdorf, column 4 the mean value of samples from broad stratigraphic horizons of the marls of Misburg/Höver, and column 5 the mean value of samples from Braunschweig and Essen. After Christensen (1988).

Goniot euthis zonation. Ernst (1964a) established a *Goniot euthis* zonation of the upper Coniacian–Lower Campanian, mainly on the basis of the mean Riedel Quotient (Text-fig. 7). The following points should be stressed:

1. In the earliest members variation of the Riedel Quotient is large and this variation gradually diminishes upwards (see column 6).

2. There is a rapid change in the mean Riedel Quotient from the upper Coniacian to the basal Lower Campanian, but virtually no change in stratigraphically younger species. The mean Riedel Quotient is about 4 during most of the Lower Campanian except in the uppermost Lower Campanian. In *G. quadrata gracilis* the mean Riedel Quotient is slightly larger than in *G. q. quadrata* from the middle Lower Campanian. This is due to the allometric relationship of the length of the guard vs the depth of the pseudoalveolus in *G. quadrata gracilis* in connection with the diminishing mean length of the guard. Due to allometry, small specimens generally have a shallower pseudoalveolus than large specimens, and consequently the mean Riedel Quotient increases when the mean length decreases. *Goniot euthis* zonation of the Lower Campanian is therefore hardly workable using only the mean Riedel Quotient. By using other characters, however, it is possible to determine samples of *Goniot euthis* with some confidence. *G. quadrata gracilis* is smaller than *G. q. quadrata*. Moreover, *G. quadrata gracilis* has notches in the pseudoalveolus and it is more strongly granulated than *G. q. quadrata* from the lower Lower Campanian.

3. Specimens with a very deep pseudoalveolus (Riedel Quotient about 2.5) occur only in the middle Lower Campanian (see column 6).

4. There is a discrepancy between the samples from Lägerdorf and Misburg/Höver in the lower and middle Lower Campanian. The samples from Misburg/Höver generally have a deeper pseudoalveolus (compare columns 3 and 4).

5. A single specimen or some few specimens cannot be assigned safely to a species. For instance, a specimen with a Riedel Quotient of 7 might belong to either *G. w. westfalica*, *G. westfalica granulata*, *G. granulata*, or *G. granulata quadrata*.

The *Goniot euthis* zonation of Ernst (1964a), was shown to be workable by Ernst (1966, 1968), Ernst and Schulz (1974), Ulbrich (1971), Christensen (1975a, b, 1986, 1988), and Jarvis (1980).

Distribution. *Goniot euthis* is known from the Middle Coniacian *I. involutus* Zone to the boundary between the Lower and Upper Campanian, and the extinction level of the genus has been proposed by several authors, including Jeletzky (1958) and Schulz *et al.* (1984), as the boundary between the Lower and Upper Campanian.

The genus had its evolutionary centre in northwestern Europe and is found almost exclusively in the Central European Palaeogeographic Subprovince. A few specimens are reported from the northernmost part of the Tethyan Realm.

Goniot euthis westfalica praewestfalica Ernst and Schulz, 1974

Plate 1, figs 10–13

1974 *Goniot euthis westfalica praewestfalica* Ernst and Schulz, p. 49, pl. 5, figs 2–9.

1983a *Goniot euthis praewestfalica* Ernst and Schulz; Bailey *et al.*, p. 35.

Holotype. The specimen figured by Ernst and Schulz (1974, pl. 5, fig. 4) is the holotype.

Material. BGS GSM 118339 from West Cliff, Ramsgate, Kent, *coranguinum* Zone, 10.0–10.5 m beneath Bedwell's Columnar Band (i.e. top Coniacian *sensu* Bailey *et al.* 1984).

Remarks. The subspecies was described in detail by Ernst and Schulz (1974) on the basis of German material. They regarded it as the earliest member of the *Goniot euthis* lineage, appearing in the Middle and Upper Coniacian chalks of Lägerdorf. They stated that *praewestfalica* can be distinguished from the nominate subspecies only on the basis of biometric analysis of a sample. The main characters separating *praewestfalica* from *westfalica* are the ventrally flattened and club-shaped guard. In addition, *praewestfalica* is not granulated, whereas *westfalica* may be granulated.

The important characters of the English specimen are as follows: length of guard, 49.1 mm; Riedel Quotient, 17.5; Slenderness Quotient, 7.2; maximum lateral diameter divided by the lateral diameter at the alveolar end, 1.2. Moreover, the specimen is not granulated. The specimen falls within the variation of *G. westfalica praewestfalica* and is from the Upper Coniacian. It is therefore referred to as *G. westfalica praewestfalica*.

Distribution. *G. westfalica praewestfalica* is recorded from NW Germany and England. It occurs in NW Germany in the Middle and Upper Coniacian (Ernst and Schulz 1974). The English specimen came from the Upper Coniacian.

Gonioteuthis westfalica westfalica (Schlüter, 1876)

Plate 1, figs 14–29

Synonymy. See Christensen (1975a).

Lectotype. The specimen figured by Schlüter (1876, pl. 53, fig. 10) was designated as lectotype by Ernst and Schulz (1974, p. 50).

Material. BMNH C44381, Micheldever, *coranguinum* Zone; BMNH C7341 and C59277, Grays, *coranguinum* Zone; BMNH C43522–3, Red Lion Pit, Gravesend, *coranguinum* Zone; BMNH C43496–9, C43502, C43504, C43510, C43518 and C43520, Gravesend, *coranguinum* Zone; BMNH C43524, Northfleet, Kent, *coranguinum* Zone; BMNH C43525, North Foreland, Kent, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C44381	46.3	3.2	6.8	5.7	7.4	14.5	6.8
BMNH C7341	56.5	1.8	8.2	7.7	9.2	31.4	6.9
BMNH C43522	50.1	3.8	7.8	7.3	9.0	13.2	6.4
BMNH C43496	65.4	4.5	9.9	9.0	10.7	14.5	6.6
BMNH C43497	54.8	6.8	11.0	9.6	11.5	8.1	5.0
BMNH C43498	60*	3.2	9.5	8.5	10.5	18.8	6.3
BMNH C43499	62.2	3.8	9.4	8.6	9.8	16.4	6.6
BMNH C43502	65.4	4.5	10.1	9.3	10.8	14.5	6.5
BMNH C43504	55.3	4.5	9.6	8.2	9.7	12.3	5.8
BMNH C43510	51.2	2.0	—	—	—	25.6	—
BMNH C43518	65.6	4.0	9.0	8.2	10.0	16.4	7.3
BMNH C43520	58*	8.2	11.6	10.3	11.0	7.1	5.0

* = estimated.

Univariate analysis. The mean value, standard deviation, coefficient of variation, and observed range of length of guard (in mm), Riedel Quotient, and Slenderness Quotient of the nine complete specimens from Gravesend are reported below.

Gravesend, Kent:

Character	N	$\bar{X}$	SD	CV	OR
L	9	59.8	5.3	8.9	51.2–65.6
RQ	9	14.8	5.6	37.7	7.1–25.6
SQ	8	6.1	0.8	13.1	5.0–7.3

Remarks. Ernst (1964a, 1968) recognized two zones of *G. westfalica* in the Lower and Middle Santonian. The lower zone is characterized by samples of *G. westfalica* having a mean Riedel Quotient above 11.5, and the upper zone by samples with a mean Riedel Quotient between 9.5–11.5 (Text-fig. 7).

The small sample from Gravesend has a mean Riedel Quotient of 14.8, suggesting the lower *G. westfalica* Zone. The large observed range of the Riedel Quotient, however, in connection with the fact that *G. westfalicagranulata* occurs at Gravesend too (see below), may indicate the presence of the upper *G. westfalica* Zone at Gravesend. The specimens from Micheldever, Grays, and the Red Lion Pit are regarded to be from the lower *G. westfalica* Zone on the basis of their Riedel Quotient.

Distribution. *G. w. westfalica* is very common in NW Germany and Scania. Outside these areas it has been recorded from most parts of the Central European Subprovince except east of Ukraine. It occurs in the Lower and Lower Middle Santonian.

Goniot euthis westfalicagranulata (Stolley, 1897)

Plate 1, figs 30–37

Synonymy. See Christensen (1975a, b).

Lectotype. The specimen figured by Stolley (1897, pl. 2, fig. 16; pl. 3, fig. 6) was designated as lectotype and refigured by Christensen (1975b, pl. 10, fig. 1; text-fig. 2A).

Material. BGS Zt1960, White Ness, near Kingsgate, Kent, uppermost *coranguinum* Zone immediately below entry of *Uintacrinus*. BMNH C43521, Gravesend, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BGS Zt1960	50.6	5.6	7.9	7.2	8.1	9.0	6.4
BMNH C43521	60*	9.0	9.9	9.2	9.2	6.7	6.1

* = estimated.

Remarks. BMNH C43521 carries granules and the Riedel Quotient is outside the range of *G. westfalica*. It is therefore tentatively referred to *G. westfalicagranulata*. Zt1960 came from beds correlative with the German *G. westfalicagranulata* Zone and falls within the variation of *G. westfalicagranulata*.

Distribution. The species occurs in the Upper Middle Santonian *G. westfalicagranulata* Zone.

Goniot euthis granulata (Blainville, 1827)

Synonymy. See Christensen (1975a).

Type. Lectotype, here designated, the original of Blainville (1827, pl. 1, fig. 10).

Material. This species occurs fairly commonly at the level of the *Marsupites* acme in east Kent and Sussex (Bailey *et al.* 1983a). I have analysed biometrically three small samples: (1) a sample labelled 'Marsupites band, Northdown brickworks pit, near Margate' (BMNH C42650–5, C42666, C42668–9); (2) a sample labelled 'Marsupites Zone, Rifle Butts, Margate' (BMNH C43250–1, C43254–7); and (3) a sample labelled 'Marsupites band, Margate' (BMNH C43242–5, C43248, C43236); all A. W. Rowe Colln.

Univariate analysis.

Northdown brickworks pit:

Character	N	$\bar{X}$	SD	CV	OR
L	9	61.3	6.8	11.1	50.7–71.6
RQ	9	6.5	0.8	11.8	5.5–7.5
SQ	9	5.7	0.5	10.6	4.8–6.4

Rifle Butts:

Character	N	$\bar{X}$	SD	CV	OR
L	6	67.3	7.2	10.7	55.0-81.0
RQ	6	7.4	1.1	15.3	6.6-9.6
SQ	6	6.2	1.1	17.7	4.9-7.9

Margate:

Character	N	$\bar{X}$	SD	CV	OR
L	6	60.8	5.4	8.9	56.3-71.2
RQ	6	7.7	1.3	16.3	6.0-9.1
SQ	6	6.2	0.7	11.0	5.1-6.9

Remarks. Ernst (1964a) recognized two zones of *G. granulata* in the Upper Santonian: a lower *Uintacrinus/granulata* Zone characterized by samples of *Goniot euthis* having a mean Riedel Quotient of 7.0-8.0, and an upper *Marsupites/granulata* Zone defined by samples of *Goniot euthis* with a mean Riedel Quotient of 6.0-7.0 (Text-fig. 7).

The three samples can be referred to *G. granulata* on the basis of their mean Riedel Quotients. The sample from Northdown brickworks pit has a mean Riedel Quotient of 6.5 and is thus from the upper Santonian *Marsupites/granulata* Zone. The samples from Rifle Butts and Margate have mean Riedel Quotients of 7.4 and 7.7, respectively, suggesting the lower Upper Santonian *Uintacrinus/granulata* Zone. This is at variance with the supposed age given on the labels, a discrepancy possibly due to the small number of specimens in the two samples.

Distribution. *G. granulata* occurs in the Upper Santonian.

Goniot euthis granulataquadrata (Stolley, 1897)

Synonymy. See Christensen (1975a, b)

Lectotype. The specimen figured by Stolley (1897, pl. 2, fig. 23; pl. 3, fig. 13) was designated as lectotype and refigured by Christensen (1975b, pl. 10, fig. 2; text-fig. 2A).

Material. BMNH C43298, C43000, C43302-4, Banham (pit no. 129 of Rowe), Norfolk.

EXPLANATION OF PLATE 2

Figs 1-27. *Goniot euthis quadrata quadrata* (Blainville), Wells, Norfolk (1-12); East Harnham, Wiltshire (13-18); and Stiffkey, Norfolk (19-27). 1-4, SM B953241, a large average-shaped specimen, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end. 5-8, SM B95375, a medium-sized specimen with an average shape; 5, dorsal view; 6, lateral view; 7, ventral view; 8, view of the anterior end. 9-12, SM B95323, a small specimen with an average shape; 9, dorsal view; 10, lateral view; 11, ventral view; 12, view of the anterior end. 13, BMNH C44308, a medium-sized guard in ventral view. 14-15, BMNH C44326, a medium-sized guard; 14, lateral view; 15, ventral view. 16-18, BMNH C44281, a large stout specimen; 16, dorsal view; 17, ventral view; 18, view of the anterior end. 19-21, SM B97232, a large specimen; 19, dorsal view; 20, dorsal view; 21, ventral view. 22-24, SM B97237, a slender medium-sized specimen; 22, dorsal view; 23, lateral view; 24, ventral view. 25-27, SM B97247, a small slender specimen; 25, dorsal view; 26, ventral view; 27, view of the anterior end, $\times 2$.

All specimens are coated with ammonium chloride. All figures are natural size unless otherwise stated.



Univariate analysis.

Character	<i>N</i>	$\bar{X}$	SD	CV	OR
L	5	68.0	9.3	13.7	59.4–80.7
RQ	5	5.5	0.8	14.1	4.2–6.1
SQ	5	6.0	0.8	13.4	5.1–6.8

Remarks. According to Ernst (1964a) *G. granulataquadrata* has a mean Riedel Quotient of 5.0–6.0 (Text-fig. 7). The small sample from Banham has a mean Riedel Quotient of 5.5 and may be referred to this species.

Distribution. *G. granulataquadrata* occurs in the basal Lower Campanian (*G. granulataquadrata* Zone).

Goniot euthis quadrata quadrata (Blainville, 1827)

Plate 2, figs 1–27

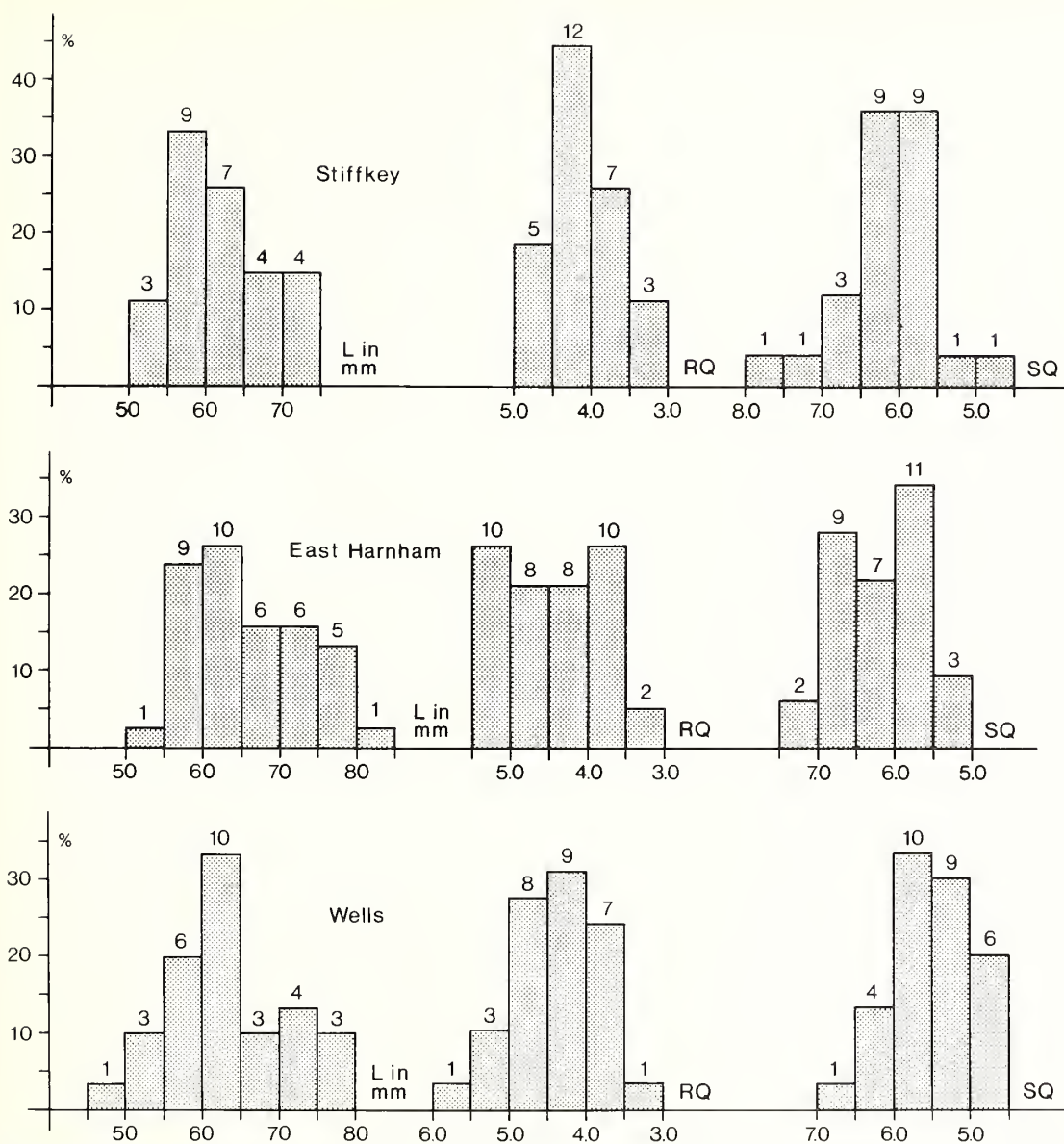
- 1827 *Belemnites quadratus* Blainville, p. 62, pl. 1, fig. 9.
 1878 *Goniot euthis quadrata* (Blainville); Bayle, pl. 23, figs 6–8.
 1892 *Actinocamax quadratus* (Blainville) var. *ampullacea* Stolley, p. 232, pl. 8, fig. 1.
 1892 *Actinocamax quadratus* (Blainville) var. *oblonga* Stolley, p. 233, pl. 7, fig. 5.
 1897 *Actinocamax quadratus* (Blainville); Stolley, p. 284, pl. 2, fig. 24; pl. 3, fig. 14.
 1952 *Goniot euthis quadrata* (Blainville) var. *cylindrica* Naidin, p. 81, pl. 5, figs 4 and 6; pl. 7, fig. 5.
 1964a *Goniot euthis quadrata quadrata* (Blainville); Ernst, pl. 1, figs 6 and 7; pl. 2, figs 5 and 6; pl. 4, fig. 1.
 1971 *Goniot euthis quadrata quadrata* (Blainville); Ulbrich, pl. 1, Reihe 1, figs 1–16, Reihe 2, figs 1–14, Reihe 3, figs 1–8.
 1980 *Goniot euthis quadrata quadrata* (Blainville); Jarvis, pl. 116, figs 1–15.
 1987 *Goniot euthis quadrata quadrata* (Blainville); Christensen and Schmid, p. 16, pl. 3, figs 8–11.

Type. Lectotype, here designated, the original of Blainville (1827, pl. 1, fig. 9).

Material. Wells: 30 near-complete specimens, *E. depressula* Subzone of the *O. pilula* Zone, Hammond Colln, SM B95314–15, B95318–24, B95328, B95330–35, B95338–39, B95341–42, B95345–47, B95351, B95353, B95367–70, B95375, B95382; Stiffkey: 27 near-complete specimens, higher part of the *Goniot euthis* Zone, Hammond Colln, SM B97232–48, B97250, B97252–56, B97263, B97268–69, B97273; East Harnham: 38 near-complete specimens, top *pilula* Zone or base of *quadrata* Zone, Blackmore Colln, BMNH C44260, C44266, C44272–73, C44275–76, C44281–87, C44290, C44293, C44299–305, C44307–09, C44314, C44322, C44326, C44330, C44332, C44336–37, C59164, C59167–68, C59170–71; Shawford, 'lower course', *quadrata* Zone: 15 near-complete specimens, Brydone Colln, BGS GSM 101087, 101090–91, 101093, 101096, 101098–103, 101106, 101108–11. In addition, I have seen many apical fragments from these localities.

Univariate analyses. The mean value, standard deviation, coefficient of variation, and observed range of the length of the guard, the Riedel Quotient, and the Slenderness Quotient are shown in Table 2. Histograms for the samples from Stiffkey, Wells, and East Harnham are shown in Text-figure 8. Histograms were not made for Shawford owing to the small number of specimens. The size-frequency distributions were tested for normality using the Kolmogorov–Smirnov test for goodness of fit, and none of the distributions differed significantly from normal (see Table 3). It should be emphasized that juvenile specimens are absent in the samples. On the basis of the univariate analyses the samples can be regarded as homogeneous.

Bivariate analyses. Scatter plots of the length of the guard vs the depth of the pseudoalveolus, and the length of the guard vs the dorso-ventral diameter at the alveolar end of the samples are shown in Text-figures 9–12, as are the regression lines. The equation of the regression lines are shown in Table 4. Values of the correlation coefficients are very highly significant ($P < 0.001$ with $N-2$ degrees of freedom). The y -intercepts were tested by the t -test to see if they differed significantly from zero. In two cases, Wells and East Harnham, the t_a -values are significant ($0.02 > P > 0.01$, with $N-2$ degrees of freedom), implying an allometric relationship of the



TEXT-FIG. 8. Histograms of the length of the guard (L), Riedel Quotient (RQ), and Slenderness Quotient (SQ) of three samples of *Goniatheuthis quadrata quadrata* from Stiffkey, East Harnham, and Wells. The figures above the bars are the actual number of specimens.

length of the guard with the dorso-ventral diameter at the alveolar end. In the other cases, the y -intercepts do not differ significantly from zero at the 5% level, implying an isometric relationship of the variates.

On the basis of these bivariate analyses, the samples are regarded as homogeneous, which is consistent with the univariate analyses.

Remarks. The mean values of the length of guard are of little taxonomic value, because juvenile specimens are absent in all samples. On the basis of the histograms and observed ranges of the

WELLS					
Character	N	$\bar{X}$	SD	CV	OR
L	30	63.8	8.2	12.8	45.1-80.0
RQ	29	4.4	0.6	14.0	3.4- 5.9
SQ	30	5.6	0.5	9.2	4.7- 6.8

EAST HARNHAM					
Character	N	$\bar{X}$	SD	CV	OR
L	38	66.3	7.3	11.0	54.0-83.3
RQ	38	4.5	0.6	13.9	3.4- 5.5
SQ	32	6.2	0.6	9.0	5.0- 7.5

SHAWFORD, 'lower course'					
Character	N	$\bar{X}$	SD	CV	OR
L	15	66.9	7.2	10.8	53.0-78.8
RQ	15	4.4	0.5	12.4	3.5- 5.4
SQ	13	6.0	0.5	7.7	5.3- 7.1

STIFFKEY					
Character	N	$\bar{X}$	SD	CV	OR
L	27	62.7	6.5	10.3	51.8-75.0
RQ	27	4.1	0.4	10.1	3.2- 4.8
SQ	25	6.2	0.6	9.4	4.9- 7.6

TABLE 2. Univariate analyses of four samples of *Gonioteuthis quadrata quadrata* from Wells, East Harnham, Shawford, 'lower course', and Stiffkey. L = length of the guard; RQ = Riedel Quotient; SQ = Slenderness Quotient; N = number of specimens, $\bar{X}$ = mean value; SD = standard deviation; CV = coefficient of variation; and OR = observed range.

length of the guard, it is obvious, nevertheless, that the specimens from Stiffkey generally are smaller than the specimens from the other samples.

The regression lines of the length of the guard *vs* the depth of the pseudoalveolus of the four samples are shown in Text-figure 13. The samples from Shawford and Wells were compared and *t*-tests showed that the two samples do not differ significantly at the 5% level. As regards Wells *vs* Stiffkey and East Harnham *vs* Stiffkey, *t*-tests showed that the positions of the regression lines are significantly different ($0.05 > P > 0.01$, with *N*-2 degrees of freedom). The specimens from Stiffkey and Shawford generally have a deeper pseudoalveolus than the specimens from Wells and East Harnham. The regression lines of the length of the guard *vs* the dorso-ventral diameter at the alveolar end of the four samples are shown in Text-figure 14 from which it is obvious that the samples from East Harnham, Shawford, and Stiffkey are virtually identical. On the other hand, the specimens from Wells are stouter. The samples from Wells and Stiffkey were compared and the *t*-

WELLS			
Character	N	D	Probability
L	30	0.1200	$P > 0.50$
RQ	29	0.0583	$P > 0.50$
SQ	30	0.1067	$P > 0.50$

EAST HARNHAM			
Character	N	D	Probability
L	38	0.1105	$P > 0.50$
RQ	38	0.1111	$P > 0.50$
SQ	32	0.1125	$P > 0.50$

STIFFKEY			
Character	N	D	Probability
L	27	0.1104	$P > 0.50$
RQ	27	0.0815	$P > 0.50$
SQ	25	0.0984	$P > 0.50$

TABLE 3. Results of the Kolmogorov-Smirnov tests for goodness of fit for three samples of *Gonioteuthis quadrata quadrata* from Wells, East Harnham, and Stiffkey.

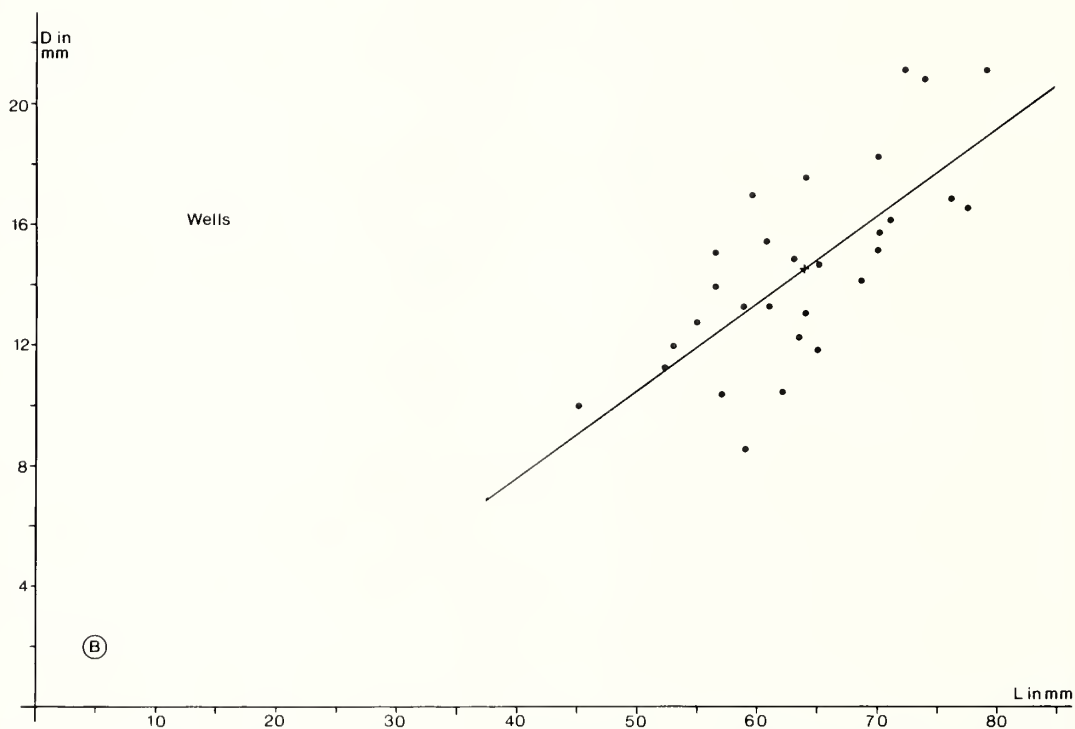
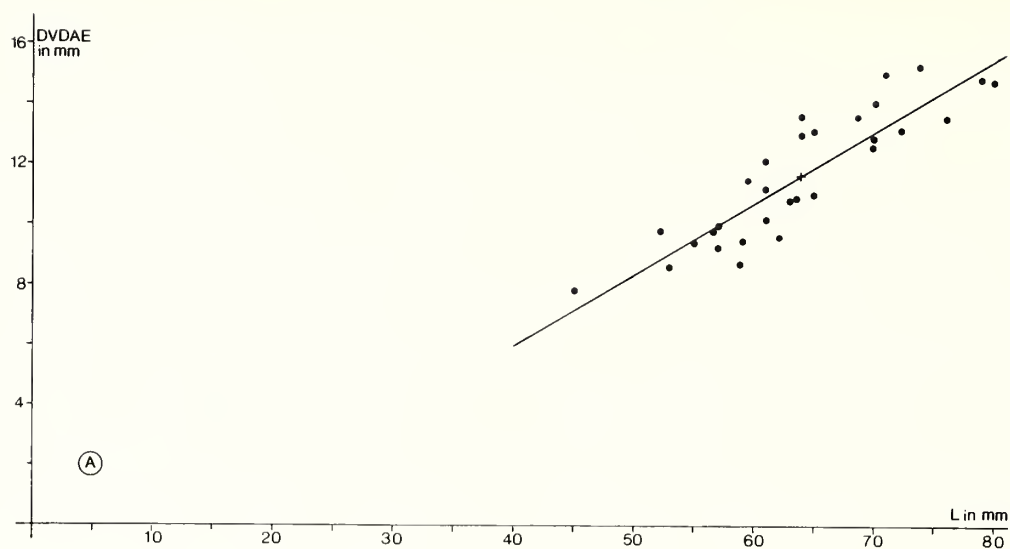
test showed that the difference of the positions is very highly significant ($P < 0.001$ with 51 degrees of freedom).

In conclusion, the specimens from Stiffkey are generally smaller, more slender, and have a deeper pseudoalveolus than the specimens from Wells. The specimens from East Harnham and Shawford are virtually identical with respect to the analysed characters. As regards the shape of the guard, the samples from East Harnham and Shawford cannot be differentiated from the sample from Stiffkey. With respect to the depth of the pseudoalveolus in relation to the length of the guard there is a slight difference between East Harnham and Stiffkey; the specimens from Stiffkey have a deeper pseudoalveolus.

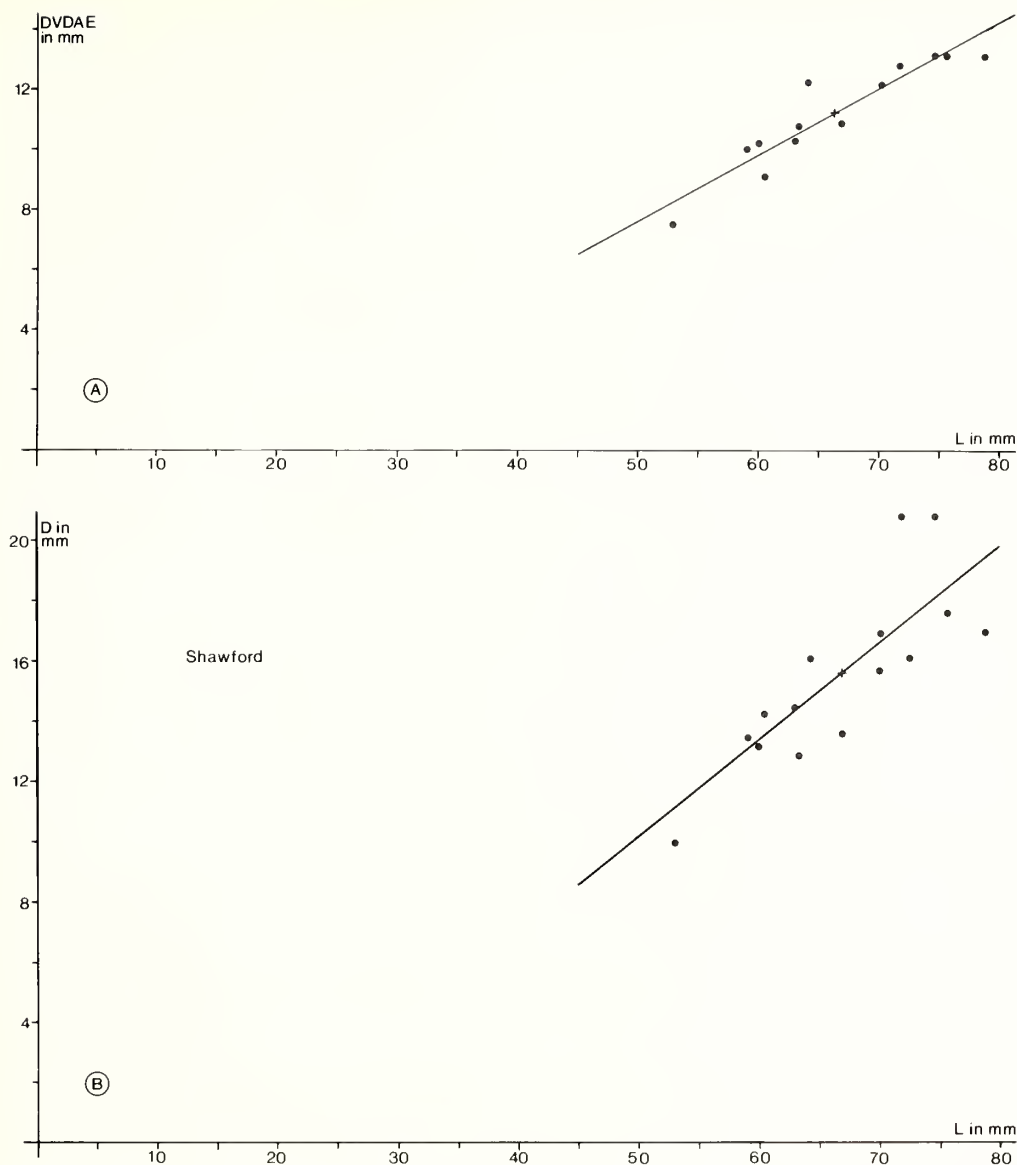
Comparisons. The four samples from England were compared to seven German samples described by Ernst (1964a, b) and two samples from Belgium and France. The sample from the C.P.L. Quarry at Hallembaye, Belgium was described by Christensen and Schmid (1987), and the sample from Hardivillers, France was described by Jarvis (1980), and was remeasured for the present study. The results of the univariate analyses of the nine samples are shown in Table 5, and the equations of the regression lines are reported in Table 6.

1. *Wells.* The sample from Wells was compared to samples of *G. q. quadrata* from Bremer and Hallembaye from the lower part of the *lingua/quadrata* Zone.

The maximum length of the guard is about 80 mm in the three samples, as in samples of *Gonioteuthis* from the lower and upper parts of the Lower Campanian of NW Germany (Ernst 1964a, fig. 8). As regards the length of the guard vs the depth of the pseudoalveolus, the sample from Wells does not differ significantly at the 5% level from the Bremer and Hallembaye samples. With regard to the length of the guard vs the dorso-ventral diameter at the alveolar end, the positions of the regression lines of the Wells and Hallembaye samples differ significantly ($0.05 > P > 0.025$, with 84 degrees of freedom). The specimens from Wells are generally stouter than the specimens from Hallembaye.



TEXT-FIG. 9. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Wells. A, length of the guard (L) vs dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) vs depth of the pseudoalveolus (D). + = mean value.



TEXT-FIG. 10. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Shawford. A, length of guard vs dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) vs depth of the pseudoalveolus (D). + = mean value.

On the basis of the comparisons made above, the sample from Wells is referred to *G. q. quadrata* and is considered to be from the lower part of the *lingua/quadrata* Zone, as are the samples from Bremer and Hallembaye.

2. *Stiffkey*. The sample from Stiffkey was compared to samples of *G. q. quadrata* and *G. quadrata gracilis* from the upper *senonensis*, *papillosa*, and *conica/gracilis* Zones of Höver/Misburg.

The maximum length of guard in the Stiffkey sample is 75 mm, as in German samples of *Gonioteuthis* from the upper part of the Lower Campanian (Ernst 1964a, fig. 8). As regards the length of the guard vs the depth

WELLS

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{y_x}	t_a	Probability
D = $-3.9641 + 0.2903L$	29	0.7387	$P < 0.001$	3.1438	0.0488	2.1277	0.9659	$0.40 > P > 0.30$
DVDAE = $-3.6437 + 0.2394L$	30	0.9025	$P < 0.001$	1.4270	0.0222	0.9745	2.5534	$0.02 > P > 0.01$

EAST HARNHAM

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{y_x}	t_a	Probability
D = $-2.7180 + 0.2697L$	38	0.6762	$P < 0.001$	3.2645	0.0491	2.1736	0.8326	$0.50 > P > 0.40$
DVDAE = $-3.7598 + 0.2203L$	32	0.8609	$P < 0.001$	1.4334	0.0219	0.8244	2.6230	$0.02 > P > 0.01$

SHAWFORD, 'lower course'

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{y_x}	t_a	Probability
D = $-5.8376 + 0.3193L$	15	0.7693	$P < 0.001$	4.9853	0.0741	2.0056	1.1710	$0.30 > P > 0.25$
DVDAE = $-3.3254 + 0.2191L$	13	0.9356	$P < 0.001$	1.6986	0.0255	0.6676	1.9577	$0.10 > P > 0.05$

STIFFKEY

$y = a + bx$	N	r	Probability	SD_a	SD_b	SD_{y_x}	t_a	Probability
D = $-4.0218 + 0.3088L$	27	0.7671	$P < 0.001$	3.2297	0.0513	1.6867	1.2453	$0.25 > P > 0.20$
DVDAE = $-2.4907 + 0.2042L$	25	0.8110	$P < 0.001$	1.9224	0.0307	0.9492	1.2956	$0.25 > P > 0.20$

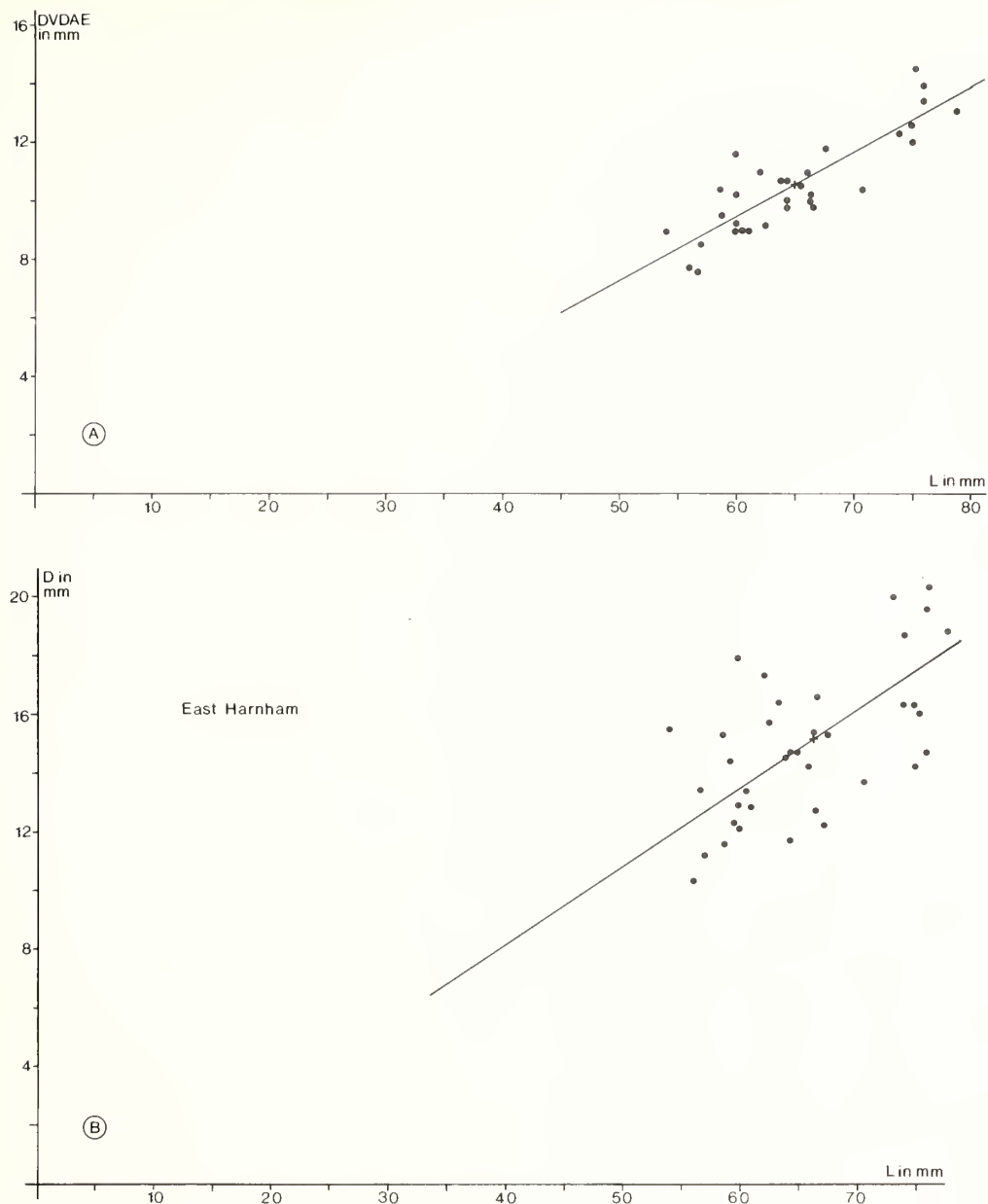
TABLE 4. Estimates of the statistical parameters of four regression analyses of samples of *Goniatites quadrata quadrata* from Wells, East Harnham, Shawford, 'lower course', and Stiffkey. L = length of the guard; D = depth of the pseudoalveolus; DVDAE = dorso-ventral diameter at the anterior end.

of the pseudoalveolus, the Stiffkey sample cannot be differentiated statistically at the 5% level from the samples from the *papillosa* and *conica/gracilis* Zones. The position of the regression lines of the samples from Stiffkey and the upper *senonensis* Zone differ significantly ($P < 0.001$, with 77 degrees of freedom). The specimens from the upper *senonensis* Zone have a deeper pseudoalveolus than the specimens from Stiffkey. With respect to the length of the guard vs the dorso-ventral diameter at the alveolar end, the Stiffkey sample cannot be differentiated statistically at the 5% level from the samples from the upper *senonensis*, *papillosa*, or *conica/gracilis* Zones.

In conclusion, the sample from Stiffkey cannot be differentiated statistically from *G. q. quadrata* from the *papillosa* Zone or *G. quadrata gracilis* from the *conica/gracilis* Zone. However, the Stiffkey belemnites do not possess notches in the pseudoalveolus, as in *G. quadrata gracilis*, and are therefore referred to *G. q. quadrata* and regarded to be from the *papillosa* Zone.

3. *East Harnham and Shawford.* The two samples are virtually identical with respect to the shape of the guard and the depth of the pseudoalveolus (see above), and therefore only the sample from East Harnham was compared with other samples of *Goniatites*.

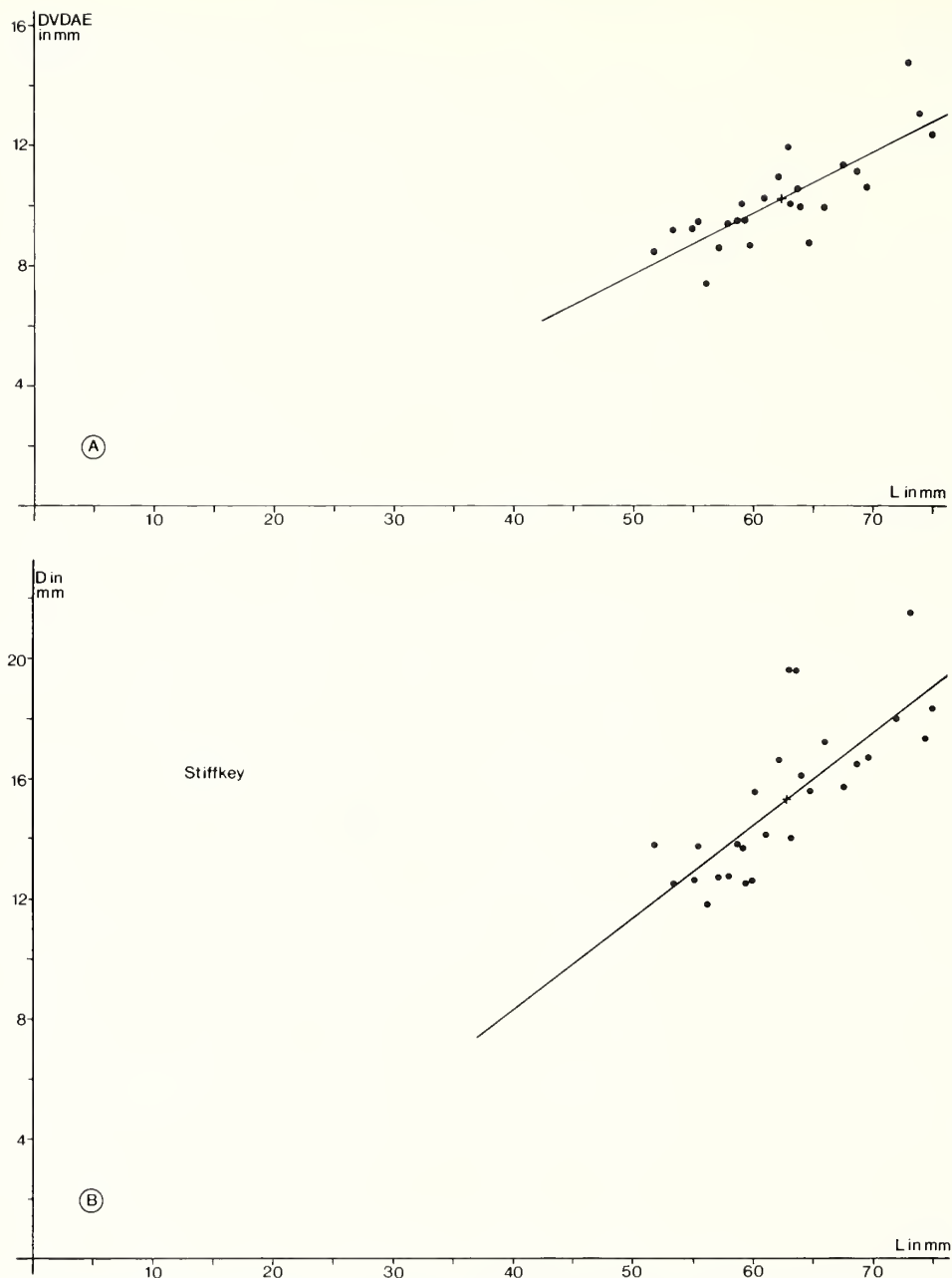
On the basis of the maximum length of the guard it is suggested that the two samples are from the middle Lower Campanian (cf. Ernst 1964a, fig. 8). As regards the length of the guard vs the depth of the pseudoalveolus, the sample from East Harnham was compared to samples of *G. q. quadrata* from Hallembaye and Bremer (lower part of the *lingua/quadrata* Zone), Höver (upper *lingua/quadrata* Zone to *pilula* Zone), and Hardivillers (*pilula* Zone *sensu anglico*), in addition to *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham sample does not differ significantly at the 5% level from the samples of *G. q. quadrata* from Hallembaye, Bremer, and Hardivillers, or *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. In the case of the comparison of East Harnham and Hallembaye, the variances were found to differ significantly ($F = 2.0100$ with 36 and 56 degrees of freedom; $0.01 > P > 0.005$); the test for non-equal



TEXT-FIG. 11. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from East Harnham. A, length of the guard (L) vs dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) vs depth of the pseudoalveolus (D). + = mean value.

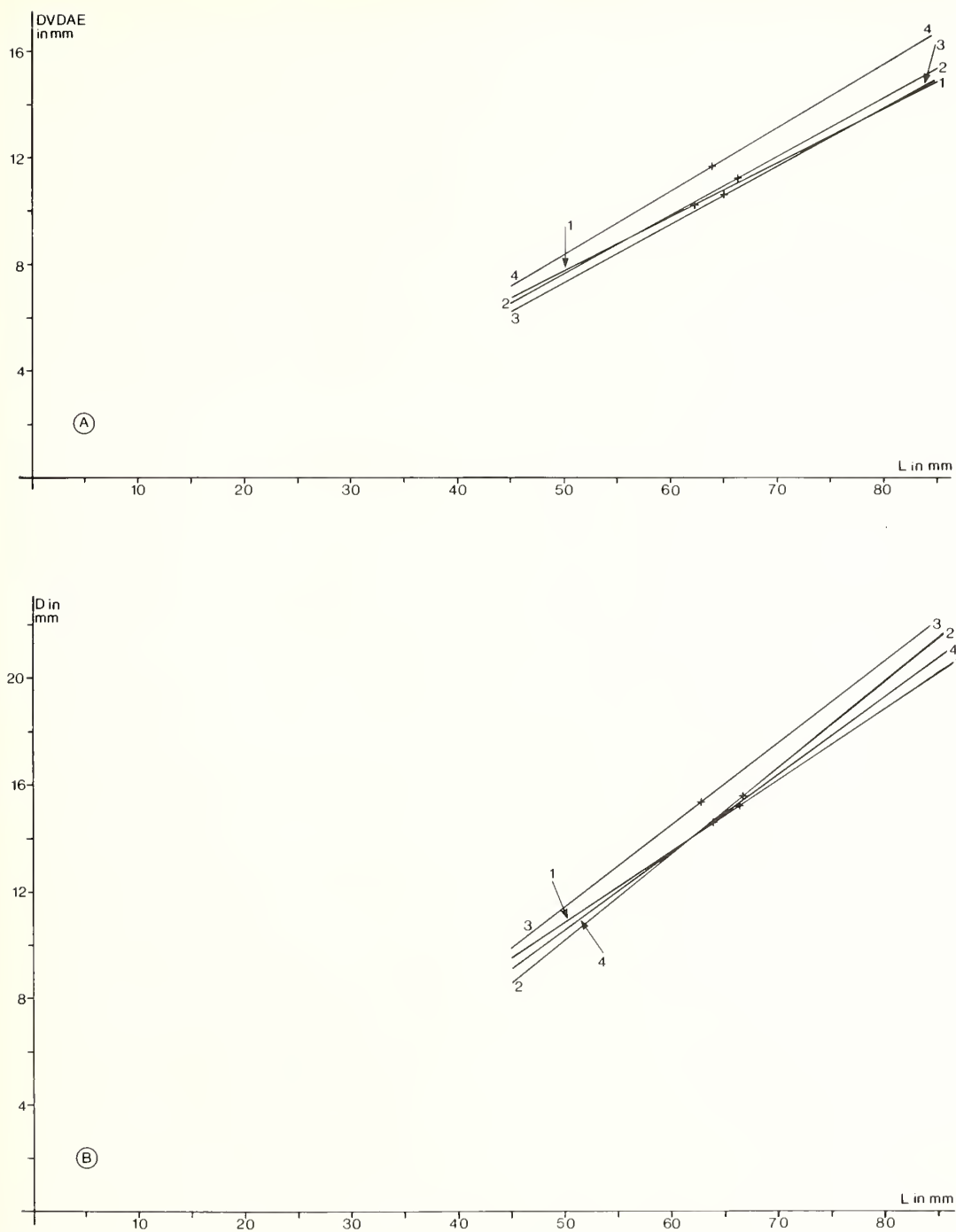
variances was therefore used. The difference of the positions of the regression lines of the samples from East Harnham and *G. q. quadrata* from the upper *lingua/quadrata* Zone to *pilula* Zone is very highly significant ($P < 0.001$ with 101 degrees of freedom); specimens from the upper *lingua/quadrata* Zone to *pilula* Zone generally have a deeper pseudoalveolus than the specimens from East Harnham.

With respect to the length of the guard vs the dorso-ventral diameter at the alveolar end, the East Harnham



TEXT-FIG. 12. Scatter plots and regression lines for *Gonioteuthis quadrata quadrata* from Stiffkey. A, length of the guard vs (L) dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) vs depth of the pseudoalveolus (D). + = mean value.

sample was compared to samples of *G. q. quadrata* from Hallembaye, Hardivillers, and the lower *senonensis* Zone of Höver, in addition to *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham sample does not differ significantly at the 5% level from the samples from Hardivillers and the *conica/gracilis* Zone. On the other hand, East Harnham vs Hallembaye and East Harnham vs the lower *senonensis* Zone of



TEXT-FIG. 13. Regression lines of four samples of *Gonioteuthis quadrata quadrata*. A, length of the guard (L) vs dorso-ventral diameter at the alveolar end (DVDAE). B, length of the guard (L) vs depth of the pseudoalveolus (D). + = mean values. 1, East Harnham; 2, Shawford; 3, Stiffkey; 4, Wells.

Höver comparisons showed that the differences in positions of the regression lines are very highly significant ($P < 0.001$). The specimens from Hallembaye and the lower *senonensis* Zone are generally stouter than the East Harnham specimens.

In conclusion, the sample from East Harnham cannot be differentiated with respect to slenderness of the guard and depth of the pseudoalveolus from samples of *G. q. quadrata* from Hardivillers, and *G. quadrata gracilis* from the *conica/gracilis* Zone of Höver. The East Harnham specimens are generally more slender than the specimens from Hallembaye and have a shallower pseudoalveolus than the specimens from the upper *lingua/quadrata* Zone to *pilula* Zone of Höver.

The samples from East Harnham, Shawford, and Hardivillers, however, are not to be referred to *G. quadrata gracilis*, because the maximum length of the guard is larger than in *G. quadrata gracilis*, and they do not possess notches in the pseudoalveolus as in *G. quadrata gracilis*. Moreover, the English top *pilula* Zone and basal *quadrata* Zone are not to be correlated with the German *conica/gracilis* Zone (see Text-fig. 1).

On the basis of the maximum length of the guard and the slenderness of the guard, in addition to the mean Riedel Quotient (4.5 in the East Harnham sample, 4.4 in the Shawford sample, and 4.3 in the Hardivillers sample) (see Table 5), the three samples are regarded as middle Lower Campanian. In samples of *G. q. quadrata* from the middle Lower Campanian of Lägerdorf the mean value of the Riedel Quotient varies from 4.2–4.5 (see Text-fig. 7); these samples have thus a more shallow pseudoalveolus than contemporaneous samples from Misburg/Höver.

Goniotenthis quadrata gracilis? (Stolley, 1892)

1892 *Actinocamax quadratus* var. *gracilis* Stolley, p. 234, pl. 7, fig. 6.

1952 *Goniotenthis quadrata* var. *gracilis* (Stolley); Naidin, p. 79, pl. 4, fig. 3; pl. 5, fig. 5; pl. 6, fig. 5.

1964a *Goniotenthis quadrata gracilis* (Stolley); Ernst, p. 166, pl. 1, fig. 8; pl. 2, figs 7–10.

Type. Lectotype, here designated, the original of Stolley (1892, pl. 7, fig. 6).

Material. BMNH C43330 from Attlebridge, and BMNH C43351 from Ringland, Norfolk.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C43330	56.6	9.9	8.7	8.0	8.0	5.7	6.5
BMNH C43351	73.9	19.9	13.1	11.8	12.4	3.7	5.6

Remarks. *G. quadrata gracilis* is distinguished from the nominate subspecies by being smaller and slenderer, with a shallower pseudoalveolus. Moreover, the edge of the pseudoalveolus often has dorsal, lateral, and ventral notches.

The two specimens from Norfolk are tentatively referred to *G. quadrata gracilis* on the basis of their slender guards. Moreover, Peake and Hancock (1961) placed Attlebridge at the top of the *Goniotenthis* Zone, and Wood (1988) placed Ringland very high in the same zone.

Distribution. *G. quadrata gracilis* occurs in the upper Lower Campanian *conica/gracilis* and *gracilis/mucronata* Zones.

Genus BELEMNELLOCAMAX Naidin, 1964

[= *Actinocamax* (*Paractinocamax*) Naidin, 1964, p. 62]

Type species. *Belemmites mammillatus* Nilsson, 1826 by original designation.

Diagnosis. See Christensen (1975a).

Remarks. The evolutionary lineage of *Belemnelloccamax*, in ascending order, *B. ex gr. grossouvrei* (Janet, 1891), *B. mammillatus* (Nilsson, 1826), and *B. balsvikensis* (Brotzen, 1960), was studied by Christensen (1975a, 1976, 1986). The general trend in evolution is the gradual calcification of the anterior end of the guard. Moreover, the guard becomes more slender and less lanceolate through time. Normally, the genus is not granulated, but a few granulated specimens of *B. ex gr. grossouvrei* and *B. mammillatus* have been recorded (cf. Christensen 1986).

BREMER, lower part of lingua/quadrata Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	38	67.3	6.4	9.5	58.5-82.5
RQ	38	4.6	0.6	13.1	3.7- 6.3
HALLEMBAYE, lower part of lingua/quadrata Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	60	67.3	7.2	10.7	52.0-80.3
RQ	58	4.5	0.5	11.1	3.5- 5.9
HÖVER, upper part of lingua/quadrata Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	24	60.3	10.5	17.4	41.0-78.5
RQ	24	4.0	0.5	12.2	2.8- 4.9
HÖVER, upper lingua/quadrata Zone to pilula Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	67	60.9	9.8	16.1	40.0-81.5
RQ	67	4.1	0.5	11.2	2.8- 5.4
HÖVER, lower senonensis Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	47	64.1	9.2	14.3	47.3-85.0
RQ	47	3.8	0.5	12.6	2.9- 4.9
HÖVER, upper senonensis Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	54	64.3	9.5	14.7	39.0-80.5
RQ	54	3.7	0.4	12.0	2.6- 4.6
HÖVER, papillosa Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	28	61.8	9.1	14.7	44.7-78.0
RQ	27	4.0	0.5	12.5	3.3- 5.0
HÖVER, conica/gracilis Zone					
Character	N	$\bar{X}$	SD	CV	OR
L	65	57.8	6.9	12.0	41.0-73.0
RQ	65	4.5	0.6	14.1	3.4- 6.4
HARDIVILLERS, middle Lower Campanian					
Character	N	$\bar{X}$	SD	CV	OR
L	61	65.8	6.7	10.2	50.0-86.6
RQ	61	4.3	0.5	12.6	3.2- 5.5

TABLE 5. Univariate analyses of nine samples of *Goniatites quadrata quadrata* and *G. quadrata gracilis*. L = length of the guard; RQ = Riedel Quotient; N = number of specimens; $\bar{X}$ = mean value; SD = standard deviation; CV = coefficient of variation; and OR = observed range.

BREMER, lower part of lingua/quadrata Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -3.1563 + 0.2687L	38	0.6924	P < 0.001	3.1534	0.0467	1.8027	1.0009	0.30 > P > 0.25	
HALLEMBAYE, lower part of lingua/quadrata Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -4.6948 + 0.2970L	58	0.8192	P < 0.001	1.8903	0.0280	1.5332	2.4836	0.02 > P > 0.01	
DVDAE = -2.4293 + 0.2136L	58	0.8326	P < 0.001	1.2636	0.0187	1.0293	1.9225	0.10 > P > 0.05	
HÖVER, upper part of lingua/quadrata Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -0.8883 + 0.2685L	24	0.7982	P < 0.001	2.6404	0.0432	2.1657	0.3364	0.80 > P > 0.70	
DVDAE = -1.8504 + 0.2018L	24	0.9193	P < 0.001	1.1258	0.0184	0.9234	1.6437	0.20 > P > 0.10	
HÖVER, upper lingua/quadrata Zone to pilula Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -1.7270 + 0.2770L	67	0.8393	P < 0.001	1.3722	0.0223	1.7695	1.2586	0.25 > P > 0.20	
DVDAE = -2.6490 + 0.2136L	67	0.9517	P < 0.001	0.5273	0.0086	0.6800	5.0236	P < 0.001	
HÖVER, lower senonensis Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -4.1994 + 0.3336L	47	0.8033	P < 0.001	2.4022	0.0371	2.3022	1.7482	0.10 > P > 0.05	
DVDAE = -1.7965 + 0.2011L	46	0.9031	P < 0.001	0.9273	0.0143	0.8886	1.9374	0.10 > P > 0.05	
HÖVER, upper senonensis Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -3.3223 + 0.3286L	54	0.8248	P < 0.001	2.0134	0.0310	2.1343	1.6501	0.20 > P > 0.10	
DVDAE = -3.4106 + 0.2224L	53	0.8960	P < 0.001	0.9749	0.0149	1.0066	3.4984	P < 0.001	
HÖVER, papillosa Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -4.9266 + 0.3353L	27	0.8582	P < 0.001	2.5120	0.0403	1.9013	1.9612	0.10 > P > 0.05	
DVDAE = -3.1714 + 0.2127L	26	0.9014	P < 0.001	1.2719	0.0205	0.8210	2.4933	0.02 > P > 0.01	
HÖVER, conica/gracilis Zone									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -3.7756 + 0.2917L	65	0.7649	P < 0.001	1.8000	0.0309	1.7110	2.0977	0.05 > P > 0.025	
DVDAE = -2.5297 + 0.2028L	65	0.9013	P < 0.001	0.7138	0.0123	0.6785	3.5442	P < 0.001	
HARDVILLERS, middle Lower Campanian									
y = a + bx	N	r	Probability	SD _a	SD _b	SD _{yz}	t _a	Probability	
D = -3.7036 + 0.2944L	61	0.7271	P < 0.001	2.2900	0.0340	1.7676	1.6173	0.20 > P > 0.10	
DVDAE = -0.6492 + 0.1778L	59	0.8146	P < 0.001	1.0922	0.0165	0.8569	0.5944	0.60 > P > 0.50	

TABLE 6. Estimates of the statistical parameters of nine regression analyses of samples of *Goniotenthis quadrata quadrata* and *G. quadrata gracilis*. L = length of the guard; D = depth of the pseudoalveolus; DVDAE = dorso-ventral diameter of the anterior end.

Naidin (1964) placed the *grossouvrei* group in *Actinocamax* (*Paractinocamax*), type species *Actinocamax grossouvrei* Janet, while *mannillatus* was placed in *Belemnelloamax*. The classification of Naidin was fully discussed by Christensen (1986) and is not followed here. The subgenus *Paractinocamax* was considered a junior synonym of *Belemnelloamax*.

Distribution. *B. ex gr. grossouvrei* is widely distributed but rare in the North European Province. *B. mannillatus* is extremely common in Scania, but rare outside this area; it has been recorded from northern Germany, Poland, and the eastern part of the Russian Platform. *B. balsvikensis* also occurs commonly in Scania, but outside this area it is unknown except for a find of two specimens from NW Germany (Christensen

and Schulz 1976). It can thus be concluded that the area of distribution of the genus *Belemnellocamax* gradually diminished through its stratigraphic range.

Belemnellocamax is recorded from the lower Santonian (possibly highest Coniacian) to the lower Upper Campanian (Christensen 1986).

Belemnellocamax ex gr. *grossouvrei* (Janet, 1891)

Plate 3, figs 1–21

Material. BMNH C42818, West Harnham, top *pilula* Zone-basal *quadrata* Zone, (holotype of *Actinocamax blackmorei* Crick, 1907); BMNH C44331 and C44254, East Harnham, top *pilula*-basal *quadrata* Zone; BGS GSM 101425, Mottisfont, top *pilula*-basal *quadrata* Zone; BMNH C44382, Micheldever, *coranguinum* Zone.

In addition to these specimens from southern England, three specimens from northern England and France are also included in the present study: (1) BMNH C46392, Ruston Parva, Yorkshire, *pilula* Zone (see Brighton 1930), (2) BMNH C10896, from flinty Chalk at Fimber, Yorkshire, *coranguinum* Zone (see Crick 1906); (3) BMNH C32498, Breteuil, France, probably top *pilula* Zone or base of *quadrata* Zone. According to I. Jarvis (in litt. 1986) this specimen most likely came from the large complex of abandoned phosphatic chalk quarries referred to as Hardivillers by Jarvis (1980).

Remarks. Specimens of the *B. grossouvrei* group are characterized by their large, ventrally flattened guards, which are lanceolate to strongly lanceolate in ventral view. Moreover, they generally have a shallow pseudoalveolus, the cross-section of which is triangular, and juvenile guards are long and elongated (Christensen 1986). About 100 specimens have been recorded from England, France, West Germany, Scania in southern Sweden, and the Russian Platform, and these specimens have been assigned to eleven species and subspecies (see Christensen 1986). The group has been the subject of excessive subdivision by earlier authors, and hopefully, the revision of this group by F. Schmid (Künzelsau) and M.-G. Schulz (Kiel) will help in solving these taxonomic problems. It should be stressed that only adult specimens have been figured previously; this may be due to the fact that juvenile and adolescent specimens are extremely rare.

Those English and French specimens of the *B. grossouvrei* group that have not been described or figured earlier, and the holotype of *A. blackmorei* are briefly commented upon below.

1. BMNH C42818. The holotype of *A. blackmorei* (Pl. 3, figs 1–4). The most anterior end of the guard is missing. It seems that the anterior end was ground, because it is completely flat and there is no trace of a shallow central pit for housing the phragmocone, or of a ventral furrow.

2. BGS GSM 101425 (Pl. 3, figs 5 and 6). An adult specimen which is strongly lanceolate in ventral view. The anterior part of the guard is badly preserved due to weathering, and the pseudoalveolus is not present.

3. BMNH C44331 (Pl. 3, figs 18–21). An adolescent specimen, which is only very slightly lanceolate in ventral view. The most anterior part of the guard is not preserved due to weathering, and only the most posterior part of the pseudoalveolus is present.

4. BMNH C44254 (Pl. 3, figs 10–13). A juvenile guard, which is strongly lanceolate in ventral and lateral views. The anterior end of the guard is flat with a pit in its centre and shows the concentric growth layers of the guard and radiating ribs. Moreover, the cross-section of the anterior end is subtriangular and a deep, short, ventral furrow is present. This specimen differs from other specimens of the *B. grossouvrei* group by having a flat anterior end. In the structure of the anterior end it resembles Turonian and early Coniacian species of *Actinocamax* (cf. Christensen 1982). The specimen is tentatively placed in the *B. grossouvrei* group due to its elongated guard which is strongly lanceolate in ventral view.

5. BMNH C44382 (Pl. 3, figs 14–17). A juvenile guard which is lanceolate in ventral view. The guard has anteriorly a shallow pseudoalveolus the cross-section of which is subtriangular. This specimen is somewhat similar to specimen no. A4331-1 (Ernst 1964a, Pl. 3, fig. 7) from the Lower Santonian of Kellermanshof near Essen, GFR. It was figured as *Gonioteuthis lundgreni/westfalica*.

6. BMNH C32498 (Pl. 3, figs 7–9). An adult specimen which is strongly lanceolate in ventral and lateral views. The guard has a shallow pseudoalveolus, the cross-section of which is subtriangular. A short ventral fissure is present.

Distribution. The stratigraphical range of the *B. grossouvrei* group was surveyed by Christensen (1986). *B. ex gr. grossouvrei* occurs in NW Germany and Scania in the basal Lower Campanian *G. granulataquadrata* Zone and the uppermost Lower Campanian *G. quadrata gracilis*/*B. mucronata* Zone or equivalent zones. In France and on the Russian Platform the group occurs in the Upper Santonian and Lower Campanian. The specimen from France commented upon above is probably from the top *pilula* Zone and/or base of the *quadrata* Zone. The two specimens from Fimber and Micheldever are from the Lower Santonian (possibly the latest Coniacian), whereas the remaining specimens are from the middle Lower Campanian (top *pilula* Zone and/or base of *quadrata* Zone). To sum up, the *grossouvrei* group occurs from the Lower Santonian (possibly the highest Coniacian) to the boundary between the Lower and Upper Campanian.

Genus BELEMNITELLA d'Orbigny, 1840

Type species. *Belemnites mucronatus* Schlotheim, 1813; ICZN Opinion 1328 (1985); name no. 2979.

Diagnosis. See Christensen (1975a).

Remarks. The International Commission on Zoological Nomenclature has designated under the plenary powers, specimen no. kca 5/2 in the collections of the Niedersächsisches Landesamt für Bodenforschung, Hannover, Germany, as neotype for *Belemnites mucronatus* Schlotheim (see ICZN 1985). The neotype was described and figured by Christensen *et al.* (1975, pl. 1, fig. 1).

Dozens of species and subspecies of *Belemnitella* from the Upper Campanian and Lower Maastrichtian have been established, and the majority of these taxa were erected on the basis of limited material by eastern European workers. The systematics of many of these taxa is in a state of disorder and they are poorly understood. Some of these taxa were discussed by Christensen (1986) and Christensen *in* Robaszynski and Christensen (1989).

Distribution. *Belemnitella* is widely distributed in the North European Province and has also been recorded from the northern part of the Tethyan Realm and the North American Province. The genus is known from the Lower Santonian to the uppermost Maastrichtian.

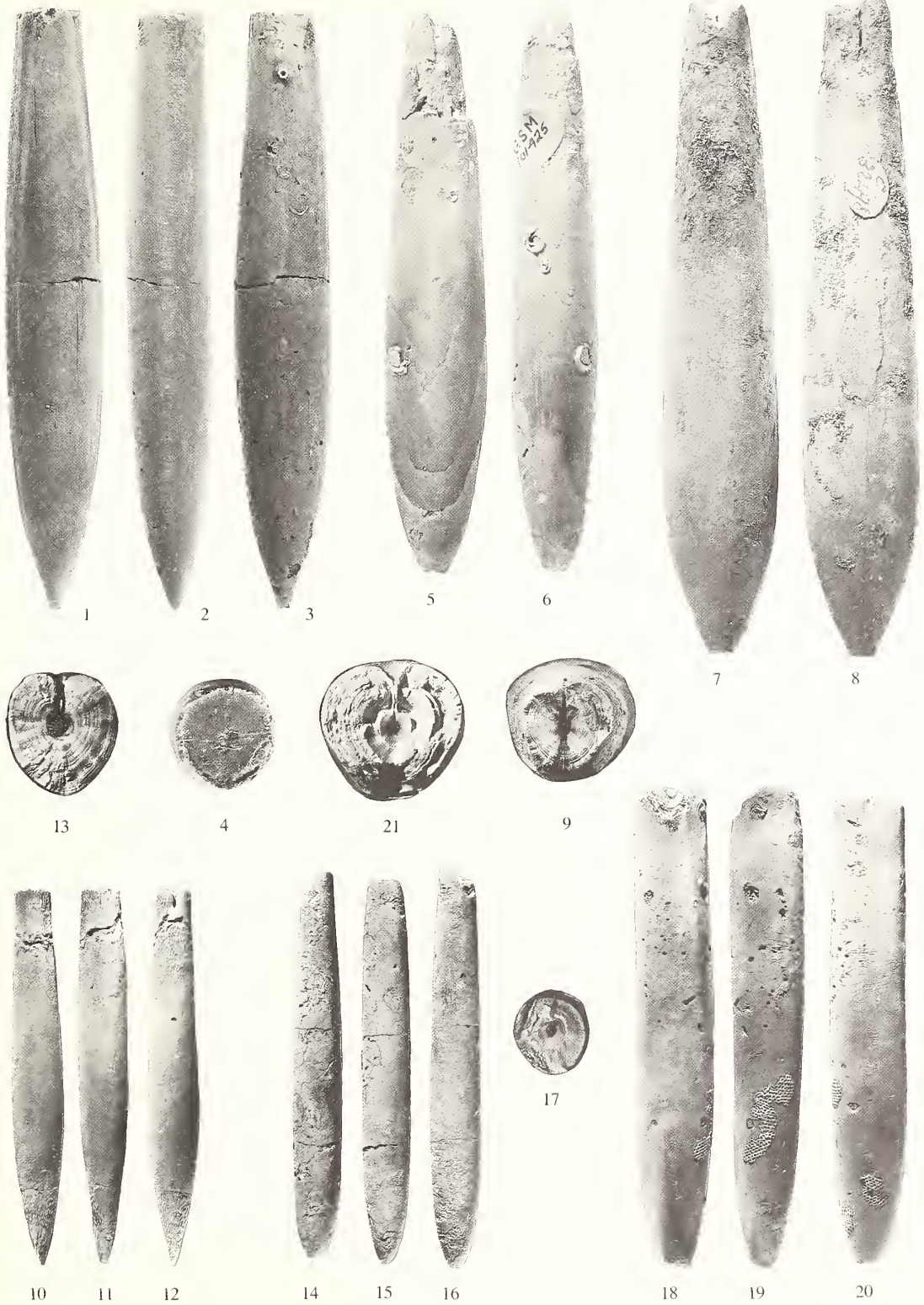
Belemnitella propinqua group

Remarks. Christensen (1986) included '*Actinocamax*' *lundgreni* Stolley from the Coniacian to Middle Santonian and *Belemnitella propinqua* (Moberg) from the Lower and Middle Santonian in

EXPLANATION OF PLATE 3

Figs 1–21. *Belemnelloamax* ex gr. *grossouvrei* (Janet) from England (1–6, 10–21) and France (7–9). 1–4, cast of holotype of *Actinocamax blackmorei* Crick, BMNH C10895 (plaster cast) and BMNH C42818, W. Harnham, top *pilula* Zone-basal *quadrata* Zone; 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end, $\times 1.5$. 5–6, BGS GSM 101425, specimen from Mottisfont, locality no. 1067 of Brydone (1914), top *pilula* Zone-basal *quadrata* Zone; 5, ventral view; 6, lateral view. 7–9, BMNH C32498, specimen from Breteuil, France, probably top *pilula* Zone-base *quadrata* Zone; the specimen probably came from the large complex of abandoned phosphatic chalk quarries, referred to as Hardvillers by Jarvis (1980); 7, dorsal view; 8, ventral view; 9, view of the anterior end, $\times 1.5$. 10–13, BMNH C44254, a juvenile specimen from East Harnham, top *pilula* Zone-basal *quadrata* Zone; note the flat anterior end with a pit in its centre, and the short, deep ventral furrow; 10, dorsal view; 11, lateral view; 12, ventral view; 13, view of the anterior end, $\times 3$. 14–17, BMNH C44382, a juvenile specimen from Micheldever, *coranguinum* Zone; 14, dorsal view; 15, lateral view; 16, ventral view; 17, view of the anterior end, $\times 2$. 18–21, BMNH C44331, a specimen from East Harnham, top *pilula* Zone-basal *quadrata* Zone; 18, dorsal view; 19, lateral view; 20, ventral view; 21, view of the anterior end, $\times 2$.

All specimens are coated with ammonium chloride. All figures are natural size unless otherwise stated.



the *Belemnitella propinqua* group. *B. propinqua* is generally considered to be the earliest representative of the genus *Belemnitella*. It is a well-defined species which was redescribed by Christensen (1971, 1973). It evolved from '*A.*' *lundgreni*.

'*A.*' *lundgreni* was placed in *Gonioteuthis* (*Goniocamax*) by Naidin (1964) together with several other species, including the earliest members of the *Gonioteuthis* lineage. This suggestion was criticized by Ernst and Schulz (1974) and Christensen (1982). Ernst and Schulz suggested that the subgenus *Goniocamax*, type species '*A.*' *lundgreni*, should be elevated to a genus or considered a subgenus of *Belemnitella*. They also suggested that only '*A.*' *lundgreni* and its ancestors should be assigned to *Goniocamax*. This suggestion must await further studies and is outside the scope of the present paper. '*A.*' *lundgreni*, however, is here placed in the *B. propinqua* group because it is closely allied to *B. propinqua*.

'*Actinocamax*' *lundgreni* Stolley, 1897

Plate 4, figs 1–6

- 1897 *Actinocamax lundgreni* Stolley, p. 285, pl. 3, figs 16–20 (*non* pl. 3, fig. 15).
- 1897 *Actinocamax mammillatus* mut. (ant.) *bornholmensis* Stolley, p. 288, pl. 4, fig. 1.
- 1897 *Actinocamax propinquus* Moberg mut. (var.) nov. Stolley, p. 295, pl. 3, fig. 23.
- 1912 *Actinocamax propinquus* Moberg; Arkhangel'sky, p. 585, pl. 10, figs 14 and 15, ? *non* 23–27, 34–36.
- 1912 *Actinocamax intermedius* Arkhangel'sky, p. 582, pl. 9, figs 30 and 31; pl. 10, fig. 6, 16–18, ? *non* 27.
- 1915 *Actinocamax plenus* Miller var. *excavata* Sinzow, p. 144, pl. 8, figs 14–17, ? *non* 18.
- 1918 *Actinocamax bornholmensis* Stolley; Ravn, p. 33, pl. 2, fig. 7.
- 1918 *Actinocamax* sp. (cfr. *Act. strehlenensis* Fritsch); Ravn, p. 34, pl. 2, fig. 8.
- 1946 *Actinocamax lundgreni* Stolley; Ravn, p. 30.
- 1949a *Belemnitella propinqua* (Moberg); Jeletzky, p. 416, text-figs 1 and 2 (*non* text-figs 3 and 4).
- 1957 *Actinocamax lundgreni lundgreni* Stolley; Birkelund, p. 13, pl. 1, figs 5 and 6.
- 1957 *Actinocamax lundgreni excavata* (Sinzow); Birkelund, p. 18, pl. 1, figs 7 and 8.
- 1957 *Actinocamax* aff. *westfalicus* (Schlüter); Birkelund, pp. 27–28, pl. 2, fig. 3.
- 1958 *Actinocamax intermedius* Arkhangel'sky; Nikitin, p. 5, pl. 1, figs 4–8.
- 1958 *Actinocamax propinquus* Moberg; Nikitin, p. 12, pl. 1, figs 9–15; pl. 3, fig. 7.
- 1964a *Gonioteuthis lundgreni*/aff. *westfalica* sensu Birkelund; Ernst, p. 161, pl. 3, figs 5 and 6.
- 1964 *Gonioteuthis* (*Goniocamax*) *lundgreni lundgreni* (Stolley); Naidin, p. 127, pl. 7, figs 5–7.
- 1964 *Gonioteuthis* (*Goniocamax*) *lundgreni excavata* (Sinzow); Naidin, p. 133, pl. 7, fig. 8.
- 1972 *Actinocamax* (*Actinocamax*) *propinquus propinquus* Moberg; Glazunova, p. 106, pl. 45, figs 1–5.
- 1972 *Actinocamax* (*Actinocamax*) aff. *propinquus propinquus* Moberg; Glazunova, p. 107, pl. 46, fig. 1.
- 1972 *Gonioteuthis* (*Goniocamax*) cf. *lundgreni lundgreni* (Stolley); Glazunova, p. 113, pl. 46, figs 3 and 4.
- 1973 *Gonioteuthis lundgreni* (Stolley); Christensen, p. 131, pl. 10, figs 6–9.
- 1974 *Gonioteuthis* (*Goniocamax*) *lundgreni lundgreni* (Stolley); Naidin, p. 211, pl. 73, fig. 8.
- 1974 *Gonioteuthis* (*Goniocamax*) *lundgreni excavata* (Sinzow); Naidin, p. 211, pl. 73, fig. 9.
- 1975a *Actinocamax lundgreni* Stolley; Christensen, p. 28.
- 1982 *Actinocamax lundgreni* Stolley; Christensen, p. 76.
- 1986 '*Actinocamax*' *lundgreni* Stolley; Christensen, p. 30.

Lectotype. The specimen figured by Stolley (1897, pl. 3, fig. 18) was designated as lectotype by Birkelund (1957, p. 4).

Material. BMNH C44380, C44383, Micheldever, Hants, *coranguinum* Zone; BMNH C43506, Gravesend, Kent, *coranguinum* Zone.

Dimensions.

	L	D	DVDAE	LDAE	MLD	RQ	SQ
BMNH C44380	49*	4.7	5.6	4.7	7.2	10.4	8.8
BMNH C44383	53*	4.2	6.4	5.6	6.8	12.6	8.3
BMNH C43506	54*	5.2	7.8	—	8.9	10.4	6.9

(* estimated)

Short description. The length of the guard is up to 70 mm. The guard is stout and lanceolate in ventral view and slightly lanceolate, subcylindrical or high conical in lateral view. It is markedly flattened ventrally and the apex is acute. The Riedel Quotient varies from about 6 to about 12, and the cross-section of the anterior end is subtriangular. The walls of the pseudoalveolus are straight or convex and often have conellae. The surface of well-preserved guards has longitudinal striae and rather prominent vascular markings.

Remarks. Stolley (1897) distinguished three taxa from the Coniacian of Bornholm: *Actinocamax lundgreni* from the 'Glass marl' at Muleby, *A. mammillatus* mut. *bornholmensis* from the Arnager Limestone west of Arnager, and *A. propinquus* mut. (var.) nov. from the marl at Stampe Å (brooklet). Ravn (1946) placed *A. mammillatus* mut. *bornholmensis* in the synonymy of *A. lundgreni*, and this view was followed by later authors, including Birkelund (1957), Jeletzky (1958), Naidin (1964), and Christensen (1973). *A. propinquus* mut. (var.) nov. is also considered a synonym of *A. lundgreni* (Christensen unpublished).

Affinity. The first member of the *Gonioteuthis* lineage, *G. westfalica praewestfalica* from the Middle and Upper Coniacian, and the first member of the *Belemnitella* lineage, '*A.*' *lundgreni* from the Lower Coniacian to Lower Santonian, are both characterized by having ventrally flattened guards which are lanceolate in ventral view. Moreover, both taxa have vascular markings and longitudinal striae. '*A.*' *lundgreni* differs, however, from *G. westfalica praewestfalica* by having a deeper pseudoalveolus and in being larger. In addition, '*A.*' *lundgreni* often has conellae on the walls of the pseudoalveolus.

Distribution. '*A.*' *lundgreni* occurs commonly on the Russian Platform, on Bornholm, Denmark, and in southern Sweden. Outside this area it is rare and has been recorded from NW Germany (Ernst 1964a; Christensen 1973, p. 133) and southern England (herein).

Christensen (1973) reviewed the biostratigraphical age of the species and concluded that it had its first occurrence in the late Coniacian and continued into the early Santonian. This was based on the assumption that the Arnager Limestone and 'Glass marl', stratum typica of '*A.*' *lundgreni* and *A. mammillatus* mut. *bornholmensis*, are of late Coniacian age. Recent studies of the inoceramid bivalve faunas of the Arnager Limestone Formation by K.-A. Tröger (Freiberg) have shown, however, that the Arnager Limestone west of Arnager is Lower Coniacian, the 'Glass marl' at Muleby is upper Lower Coniacian, and the marl at Stampe Å is lower Middle Coniacian in inoceramid terms. On ammonite evidence, however, the Arnager Limestone west of Arnager is at least Middle Coniacian (Kennedy and Christensen 1991). '*A.*' *lundgreni* also occurs together with *G. westfalica* and *Belemnitella propinqua* in parts of the Bavnodde Greensand Formation which is Lower Santonian (Christensen unpublished). It can thus be concluded that the stratigraphic range of '*A.*' *lundgreni* is Lower Coniacian to Lower Santonian.

'*Actinocamax*' ex gr. *lundgreni* Stolley, 1897

Plate 4, figs 7–12

1907 *Actinocamax* sp. Crick, p. 392, text-fig. 2.

Material. BMNH C10576, Fletcher and Co's Pit, Gravesend, Kent, *coranguinum* Zone; BMNH C59278, Grays, Essex, *coranguinum* Zone.

Short description. BMNH C10576 is a 70.6 mm long fragment, consisting of approximately the anterior two-thirds of the guard. It is estimated that the total length of the guard may have been 105–110 mm. It is lanceolate

in ventral view and subcylindrical in lateral view. The guard has anteriorly a shallow pseudoalveolus 15 mm deep. The cross-section of the anterior end is subtriangular and the walls of the pseudoalveolus are covered by large, closely spaced conellae. Ventrally the guard is flattened and the surface of the guard is smooth.

BMNH C59278 is 54 mm long, but the most anterior part of the guard is not preserved. It is lanceolate in ventral view and slightly lanceolate in lateral view. The guard has anteriorly a shallow pseudoalveolus with walls covered by conellae. The depth of the preserved part of the pseudoalveolus is 6.8 mm and the cross-section of the alveolar end seems to have been subtriangular. Ventrally the guard is markedly flattened and the surface is smooth.

Remarks. BMNH C10576 was fully described by Crick (1907) who assigned it to *Actinocamax* sp., after having discussed its affinity to the *grossouvrei* group. Later on, it was assigned to the *Mammillata* group by Jeletzky (1949b), the *grossouvrei* group by Christensen (1975a), and possibly the '*A.*' *lundgreni* group by Christensen (1986). C10576 shares many characters with the *grossouvrei* group, including the size, shape and ventral flattening of the guard, the cross-section of the alveolar end, and the surface sculpture. It has, however, a deeper pseudoalveolus than the *grossouvrei* group, and it is estimated that the Riedel Quotient may have been about 7. In addition, it has many closely spaced conellae. C10576 resembles '*A.*' *lundgreni* in the shape and ventral flattening of the guard, and the depth of the pseudoalveolus. It is, however, larger than '*A.*' *lundgreni*. On the basis of the depth of the pseudoalveolus, it is tentatively referred to as '*A.*' ex gr. *lundgreni*.

BMNH C59278 also has characters in common with the *grossouvrei* group and '*A.*' *lundgreni*. On the basis of the depth of the pseudoalveolus (Riedel Quotient estimated to be about 5) it is tentatively referred to as '*A.*' ex gr. *lundgreni*.

Distribution. The specimens from Grays and Gravesend are considered to be from the Lower Santonian (see above).

Belemnitella propinqua propinqua (Moberg, 1885)

Plate 4, figs 13–18; Plate 5, figs 11–14

Synonymy. See Christensen (1971).

Holotype. By monotypy the specimen figured by Moberg (1885, pl. 5, fig. 25). It was refigured by Christensen (1971, pl. 1, fig. 1).

Material. BMNH C5502, Grays, Essex, *coranguinum* Zone; BMNH C43508 and C43519, Gravesend, Kent, *coranguinum* Zone.

EXPLANATION OF PLATE 4

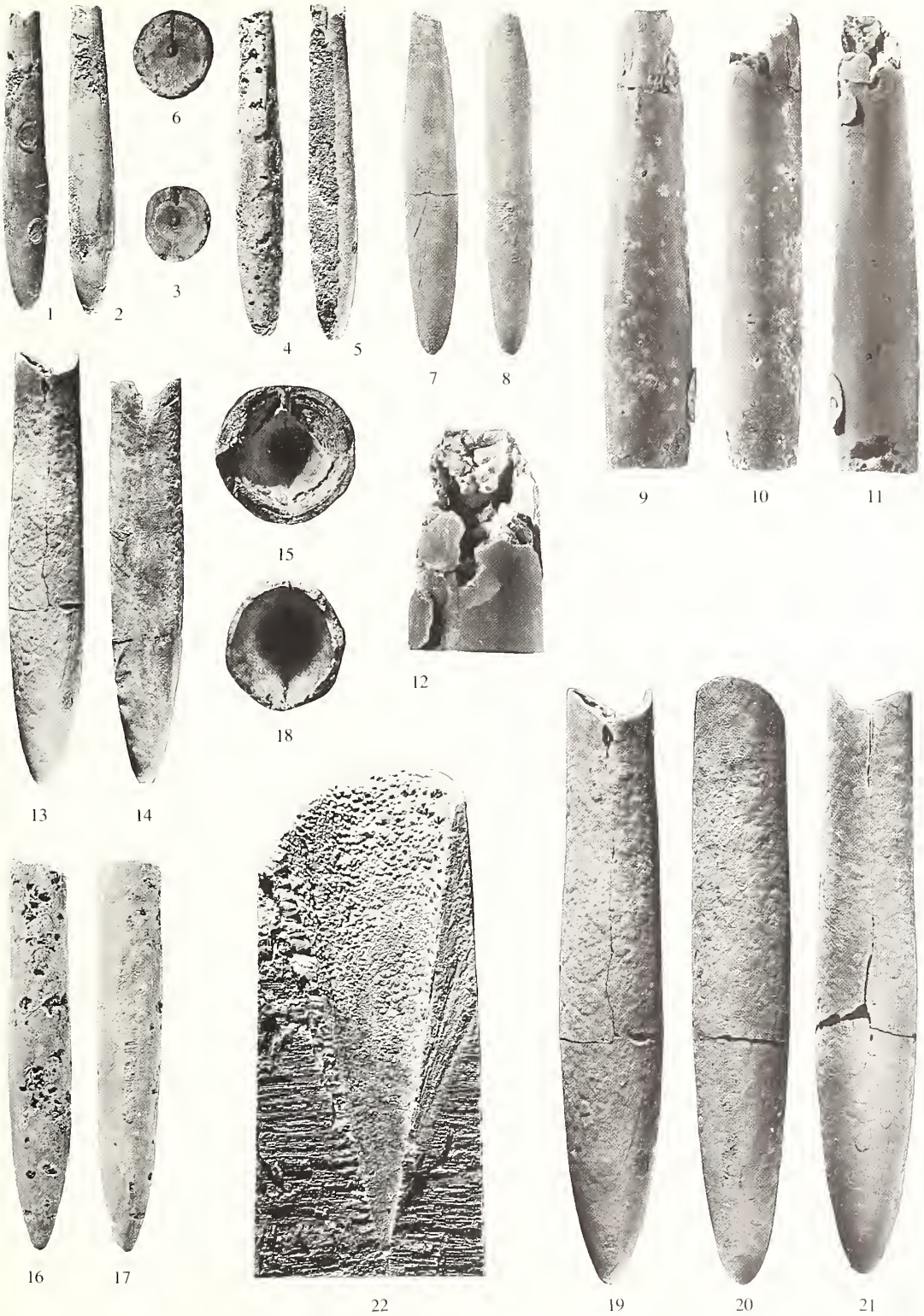
Figs 1–6, '*Actinocamax*' *lundgreni* Stolley. 1–3, BMNH C44380, Micheldever, *coranguinum* Zone; 1, dorsal view; 2, ventral view; 3, view of the anterior end, $\times 2$. 4–6, BMNH C44383, Micheldever, *coranguinum* Zone; 4, dorsal view; 5, ventral view; 6, view of the anterior end, $\times 2$.

Figs 7–12, '*Actinocamax*' ex gr. *lundgreni* Stolley. 7–8, BMNH C59278, Grays, *coranguinum* Zone; 7, dorsal view; 8, lateral view. 9–12, BMNH C10576, Fletcher and Co's Pit, Gravesend, *coranguinum* Zone; specimen figured as *Actinocamax* sp. by Crick (1907, text-fig. 2); 9, dorsal view; 10, lateral view; 11, ventral view; 12, view of the anterior end showing conellae, $\times 2$.

Figs 13–18, *Belemnitella propinqua* (Moberg). 13–15, BMNH C43519, Gravesend, *coranguinum* Zone; 13, dorsal view; 14, ventral view; 15, view of the anterior end, $\times 2$. 16–18, BMNH C5502, Grays, *coranguinum* Zone; 16, dorsal view; 17, lateral view; 18, view of the anterior end, $\times 2$.

Figs 19–22, *Belemnitella* cf. *praecursor* Stolley, BMNH C43288, Porchester Pit, Hampshire; specimen labelled '*mucronata*' Zone, but according to Griffith and Brydone (1911) this pit is placed in the Subzone of *G. quadrata*; 19, dorsal view; 20, lateral view; 21, ventral view; 22, view of the split anterior end showing conellae, c. $\times 2.5$.

All specimens are coated with ammonian chloride, except figs 9–12, and are natural size unless otherwise stated.



CHRISTENSEN, '*Actinocamax*', *Belemnitella*

Short description. A *Belemnitella* with a rather sturdy guard, lanceolate in ventral view and slightly lanceolate or subcylindrical in lateral view. The cross-section of the pseudoalveolus at the alveolar end is subtriangular to pointed oval. The walls of the pseudoalveolus are covered by closely spaced concellae. The Riedel Quotient varies from a little less than three to about four.

The most anterior part of the guard in C43508 and C43519 is not preserved. It is estimated that the Riedel Quotient is about 4 in C43508 and about 3 in C43519.

Dimensions.

	L	D	DVDAE	LDAE	MLD	LVF	RQ	SQ
BMNH C5502	60.5	19.6	10.0	8.9	10.2	6.0	3.1	6.1

Remarks. Christensen (1971, 1973) described the species in detail on the basis of Swedish and Danish material, including the holotype. Christensen (1971) listed synonyms and showed that the species had been misinterpreted by Russian palaeontologists. The following taxa were considered to be synonyms of *B. p. propinqua*: *Actinocamax propinquus*? Moberg, 1885, *Belemnitella mucronata* mut. anterior Stolley, 1897, *B. ex gr. mirabilis* Jeletzky, 1948, *A. propinquus ravni* Birkelund, 1957, *Gonioteuthis jeletzkyi* Kongiel, 1962, and *B. rylskiana* Nikitin, 1958.

Naidin (1974) employed a different concept of *B. p. propinqua* from that of Christensen (1971, 1973, 1986, and herein). He recognized *B. p. propinqua* from the Lower Santonian and *B. propinqua rylskiana* from the upper Lower to Upper Santonian, in addition to the dubious *B. propinqua mirabilis* Arkhangelsky, 1912 from the Santonian of northern Kazakhstan.

Distribution. *B. p. propinqua* occurs on the Russian Platform, on Bornholm, Denmark, and in southern Sweden. Outside this area it has only been recorded from southern England (herein). It occurs in the Lower and Middle Santonian.

Belemnitella praecursor group

Remarks. Christensen (1986) tentatively placed *B. alpha* Naidin and *B. praecursor* Stolley from the lower and middle Lower Campanian in this group. The two taxa were fully discussed, including their mutual relationship, and their relationship to *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian (see also Christensen 1975a; Christensen and Schmid 1987).

B. praecursor differs from *B. alpha* in several characters (see below), but it should be stressed that it is not possible on the basis of only a few specimens to assign them safely to either *B. praecursor* or *B. alpha* because the range of variation overlaps.

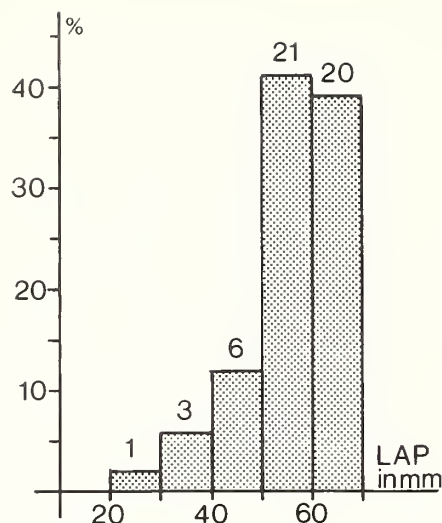
EXPLANATION OF PLATE 5

Figs 1–10. *Belemnitella praecursor* Stolley. 1–2, BMNH C43960, East Harnham, top *pihula* Zone-basal *quadrata* Zone; 1, lateral view; 2, ventral view. 3–4, BMNH C43964, East Harnham, top *pihula* Zone-basal *quadrata* Zone; a smooth and slender specimen; 3, lateral view; 4, ventral view. 5–7, BMNH C44149, East Harnham, top *pihula* Zone-basal *quadrata* Zone; specimen figured as *B. lanceolata* by Blackmore (1896, pl. 1, fig. 1); 5, dorsal view; 6, lateral view; 7, ventral view. 8–10, BMNH C43954, East Harnham, top *pihula* Zone-basal *quadrata* Zone; 8, dorsal view; 9, lateral view; 10, ventral view.

Figs 11–14. *Belemnitella propinqua* (Moberg), BMNH C43508, Gravesend, *coranguinum* Zone; 11, dorsal view; 12, lateral view; 13, ventral view; 14, view of the anterior end, $\times 2$.

All specimens are coated with ammonium chloride, and are natural size unless otherwise stated.





TEXT-FIG. 14. Histogram of the length from apex to the protoconch (LAP) of *Belemnitella praecursor* from East Harnham. The figures above the bars are the actual number of specimens.

Belemnitella praecursor Stolley, 1897

Plate 5, figs 1-10; Plate 6, figs 1-4, 8-10

Synonymy. See Christensen and Schmid (1987).

Holotype. By monotypy the original of Stolley (1897, pl. 3, fig. 24). A cast of the holotype was figured by Christensen (1986, pl. 3, fig. 4) and Christensen and Schmid (1987, pl. 3, figs 4 and 5).

Material. 82 specimens (BMNH C5776, C43953-67, C43972-80, C43986-44007, C44009-31, C44134, C44160-2, C44245, and C59152-8) from East Harnham, top *pilula* Zone-basal *quadrata* Zone.

Description. The guard is long, well-preserved guards ranging up to 150 mm. In ventral view the guard is generally lanceolate with a constriction at the base of the ventral fissure, and in lateral view it is high conical. The guard is flattened ventrally over its entire length. The apical angle is acute in both juvenile and adult specimens, and the mucro is only slightly delimited.

The guard is slender; the ratio of the length from apex to protoconch and the dorso-ventral diameter at the protoconch varies from about 3 to about 6, being 3.4-4.6 in most specimens, and the mean value is about 4.

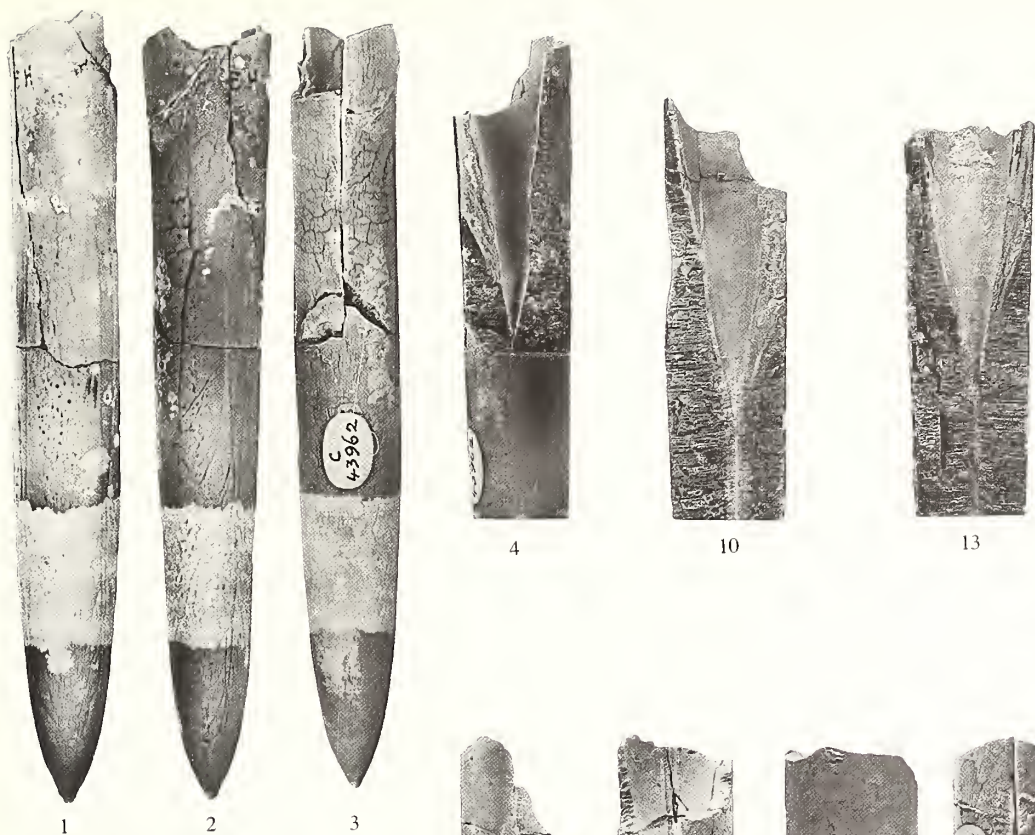
The depth of the alveolus is about half the length of the guard in well-preserved specimens. The shape of the bottom of the ventral fissure is generally straight or almost straight, but it may also be straight with an outward bend, S-shaped, curve, or undulating. The walls of the alveolus may be covered by conellae. The fissure angle and Schatzky distance are small, and the alveolar angle varies from 18-22° (see below).

EXPLANATION OF PLATE 6

Figs 1-4, 8-10. *Belemnitella praecursor* Stolley. 1-4, BMNH C43962, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the anterior end showing internal characters. 8-10, BMNH C59154, East Harnham, top *pilula* Zone-basal *quadrata* Zone; 8, lateral view; 9, ventral view; 10, view of the split anterior end showing internal characters.

Figs 5-7, 11-13. *Belemnitella* cf. *praecursor* Stolley. 5-7, SM B97228, Stiffkey, *quadrata* Zone; 5, dorsal view; 6, lateral view; 7, ventral view. 11-13, BGS GSM 101391, Shawford, *quadrata* Zone; 11, lateral view; 12, ventral view; 13, view of the split anterior end showing internal characters.

All specimens are coated with ammonium chloride, and are natural size.



Juvenile specimens are, by and large, smooth. Adolescent and adult specimens have weakly developed vascular markings, in addition to dorso-lateral depressions, dorso-lateral double furrows and longitudinal striae. The vascular markings are most prominent around the ventral fissure, and the longitudinal striae are typically more distinct than the vascular markings.

Biometry. A sample of *B. praecursor* from East Harnham was analysed by univariate and bivariate methods. Only very few specimens were split in the median plane, and thus the internal characters are known in fewer than ten specimens. The length from the apex to the protoconch was measured in unsplit specimens.

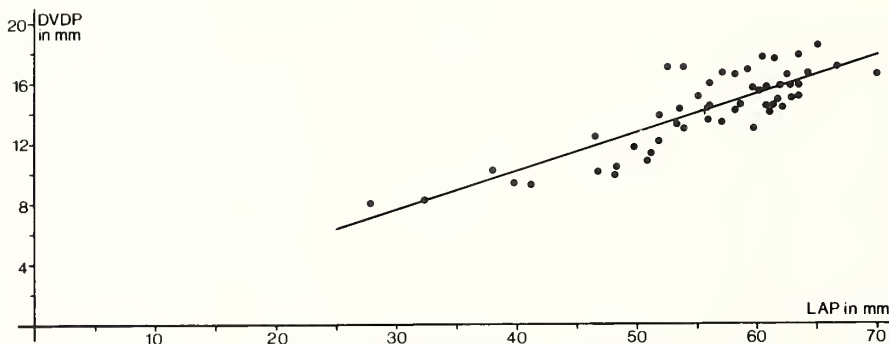
B. praecursor from East Harnham:

Character	<i>N</i>	$\bar{X}$	SD	CV	OR
LAP	51	55.6	8.6	15.5	27.8–69.9
DVDP	51	14.2	2.7	19.0	8.1–18.6
SD	8	8.2	1.9	22.8	6.4–11.3
FA	9	15.2	5.5	36.4	7.0–23.0
AA	8	20.2	0.6	2.9	19.5–21.5
LAP/DVDP	51	4.0	0.4	10.2	3.1–4.8

A histogram of the length from apex to protoconch is shown in Text-figure 14. It was tested for normality using the Kolmogorov–Smirnov-test for goodness of fit, and the test showed that the size-frequency distribution does not differ significantly from normality at the 5% level ($D = 0.1361$; $0.5 > P > 0.2$ with 51 degrees of freedom).

Bivariate analysis. The scatter plot of the length from the apex to the protoconch vs the dorso-ventral diameter at the protoconch is shown in Text-figure 15, as is the regression line. The value of the correlation coefficient is very highly significant ($P < 0.001$ with 49 degrees of freedom). A *t*-test on the *y*-intercept gave a value of 0.1289 with 49 degrees of freedom which is not significant ($0.9 > P > 0.8$), implying an isometric relationship of the variates.

On the basis of the univariate and bivariate analyses the sample from East Harnham can be regarded as homogeneous.



TEXT-FIG. 15. Scatter plot and regression line for *Belemnites praecursor* from East Harnham. LAP = length from apex to the protoconch; DVDP = dorso-ventral diameter at the protoconch; + = mean value.

$$\text{DVDP} = -0.1777 + 0.2567 \text{ LAP}; N = 51; r = 0.8347; \text{SD}_a = 1.3782; \text{SD}_b = 0.0239; \text{SD}_{yx} = 1.4542.$$

Remarks. *B. praecursor* was established on the basis of only one specimen and characterized as being smooth (Stolley 1897). Later Jeletzky (1955a) discussed the concept of *B. praecursor* and established two varieties, var. *media* and var. *mucronatiformis*, in addition to var. *praecursor*. He failed, unfortunately, to present appropriate biometrical data and/or a differential diagnosis for the three varieties.

Christensen and Schmid (1987) analysed the variation of the critical characters in a large sample of *B. praecursor* from the Vaals Formation (lower Lower Campanian, lower part of the *I. lingua*/*G. quadrata* Zone *sensu germanico*) of the C.P.L. Quarry at Hallembaye, Belgium. The results of the univariate and bivariate biometric analyses of the Hallembaye sample are reported below for comparison.

B. praecursor from Hallembaye (Christensen and Schmid 1987): *Univariate analysis*.

Character	N	$\bar{X}$	SD	CV	OR
LAP	46	60.9	11.8	19.4	20.1–79.2
DVDP	60	15.3	3.6	23.3	4.9–19.0
SD	57	6.4	1.3	20.9	4.2–10.2
FA	52	17.6	5.0	28.2	10.0–28.0
AA	59	20.1	0.9	4.3	18.0–22.0
LAP/DVDP	46	4.1	0.5	12.7	3.1–5.9

Bivariate analysis.

DVDP = $-2.0831 + 0.2854 \text{ LAP}$; $N = 46$; $r = 0.9208$; $\text{SD}_a = 0.6684$; $\text{SD}_b = 0.0108$; $\text{SD}_{yx} = 0.8534$.

The relationship of the length from the apex to the protoconch *vs* the dorso-ventral diameter at the protoconch of this sample is very strongly allometric, and the juvenile and adolescent specimens are more slender than the adult specimens (Christensen and Schmid 1987).

The sample from East Harnham is closely similar to the sample from Hallembaye with respect to slenderness and shape of the guard, surface sculpture, Schatzky distance and fissure angle. The East Harnham sample differs, however, from the Hallembaye sample in two ways: (1) the guard is generally slightly smaller, and (2) the relationship of the length from the apex to the protoconch *vs* the dorso-ventral diameter at the protoconch is isometric. Christensen (1986) and Christensen and Schmid (1987) considered the allometry to be diagnostic for the species. This assumption is now known to be incorrect.

The three varieties of *B. praecursor*, which '...are only morphologically varieties of the same specific type (parts of the same populations...)' (Jeletzky 1955a, p. 482), must be treated as subspecies, following Article 45g of the International Code of Zoological Nomenclature (1985), because they have been used as subspecies in papers published before 1985. Christensen and Schmid (1987), however, did not recognize subspecies of *B. praecursor*, and subspecies are not recognized in the present paper. Extreme variants with a smooth guard, referred to as var. *praecursor* by Jeletzky, do occur in the East Harnham sample (see Pl. 5, figs 3 and 4).

Affinity. *B. praecursor* is closely allied to *B. alpha* Naidin from the lower and middle Lower Campanian, and *B. mucronata* (Schlotheim) from the uppermost Lower Campanian and Upper Campanian. The affinity was fully discussed by Christensen (1986) and Christensen and Schmid (1987). *B. praecursor* differs from *B. alpha* by being more slender, having a smaller Schatzky distance, and a larger fissure angle. Moreover, in *B. praecursor* the ratio of the length from the apex to the protoconch and the dorso-ventral diameter at the protoconch varies from about 3 to about 6, generally being 3.6–4.6, and the mean value is 4. In *B. alpha*, the ratio varies from about 3 to about 4, being 3.2–3.8 in most specimens, and the mean value is 3.5.

B. praecursor differs from *B. mucronata* by having weakly developed vascular markings, lacking a well-defined mucro, and being longer and more slender. The fissure angles of *B. mucronata* from the uppermost Lower Campanian and basal Upper Campanian and *B. praecursor* are very similar, whereas samples of *B. mucronata* from the middle Upper Campanian generally have larger fissure angles.

Distribution. *B. praecursor* has been recorded from Northern Ireland, through England, France, Belgium, northern Germany, Poland to Russia (Christensen 1986; Christensen and Schmid 1987).

The specimens from East Harnham are regarded to be from the middle Lower Campanian (see above). *B.*

praecursor occurs in West Germany in the lower Lower Campanian *G. granulataquadrata* Zone and the overlying *I. lingua/G. quadrata* Zone. A single specimen has also been collected in the middle Lower Campanian *Galeola senouensis* Zone. In Belgium, it occurs in the lower part of the *I. lingua/G. quadrata* Zone of the basal Lower Campanian. In Northern Ireland and southern England it occurs in the middle Lower Campanian. In Russia, *B. praecursor* appears in the uppermost Santonian and continues into the lower and middle Lower Campanian (Naidin and Kopaevich 1977; Naidin 1979, 1983). In the Corbières area of the French Pyrenees *B. praecursor* has recently been recorded from the uppermost Santonian (Christensen *et al.* 1991). Jeletzky (1955*b*) recorded a single specimen from the U.S.A. which probably came from the Niobrara Formation in Kansas.

Belemnitella cf. praecursor

Plate 4, figs 19–22; Plate 6, figs 5–7, 11–13

Material. BMNH C43288, Porchester Pit, Portsdown Hills, Hampshire; SM B97228–31, Stiffkey; BGS GSM 101370, 101376, 101379–81, Shawford.

Dimensions.

	LAP	DVDP	LDP	SD	FA	AA	LAP/DVDP
BMNH C43288	61.8	15.3	15.3	6.4	21.5	23.0	4.0
SM B97231	59.0	14.8	14.2	—	—	—	4.0
SM B97228	50.6	13.6	13.7	—	—	—	3.7
SM B97230	48.4	12.5	—	10.6	—	—	3.9
SM B97229	36.6	8.8	8.3	—	—	—	4.2
BGS GSM 101370	64.3	15.3	15.6	—	—	—	4.2
BGS GSM 101376	38.7	8.7	8.2	—	—	—	4.5
BGS GSM 101379	64.6	15.4	15.3	—	—	—	4.2
BGS GSM 101380	53.4	13.1	13.1	—	—	—	4.1
BGS GSM 101381	57.8	15.5	15.2	—	—	—	3.7

Remarks. The specimen from Porchester Pit is relatively slender (LAP/DVDP is 4.0), has weakly developed vascular imprints, and no well-defined mucro. The alveolus carries conellae (Pl. 4, figs 19–22) as in *B. praecursor* and *B. alpha*. The specimens from Stiffkey have weakly developed vascular imprints and the mucro is not well-defined. The mean value of the LAP/DVDP ratio of four specimens is 3.9, with an observed range from 3.7–4.2. The specimens from Porchester Pit and Stiffkey may be *B. praecursor* on the basis of their LAP/DVDP ratios, but they are referred to *B. cf. praecursor* owing to the small number of specimens.

I have also studied a small *Belemnitella* sample from Shawford, locality 1086 of Brydone (1912). Most of the specimens are unhorizoned, and the remaining specimens are from 'bottom course', 'lower course', '2nd course', and 'below upper marl layers' *sensu* Brydone. The *Belemnitella* fauna is heterogeneous in contrast to the *Belemnitella* sample from East Harnham (see above). It seems that specimens of *Belemnitella* from several horizons within the middle and upper Lower Campanian are present. Five specimens from the 'bottom course' and 'lower course' are referred to *B. cf. praecursor* on the shape and slenderness of the guard (the mean value of the LAP/DVDP ratios is 4.1 with an observed range of 3.7–4.5), and the weakly developed vascular markings. Some of the unhorizoned specimens may also be *B. cf. praecursor*. *B. mucronata*, however, is also present and this species appears in the uppermost Lower Campanian. The specimens of *B. mucronata*, however, may have come from another pit.

Distribution. The specimens from Stiffkey are regarded as coming from the upper Lower Campanian *papillosa* Zone (see above), and the specimens from Shawford from the middle Lower Campanian.

Belemnitella sp.

Material. SM B95274, Wells, *pilula* Zone; BMNH C44865, Sussex coast, base of *G. quadrata* Zone.

Remarks. SM B95274 is a fragment of a juvenile specimen consisting of the middle part of the guard. BMNH C44865 is a stout specimen (LAP: DVDP is 3.5) with vascular imprints. It was recorded as *Actinocamax mercyi* by Rowe (1900, p. 343). A specific determination of the two specimens is not possible.

Acknowledgements. This paper is dedicated to the memory of Tove Birkelund (1928–1986) in token of her contribution to Mesozoic stratigraphy and palaeontology. Tove's first field of activity was Upper Cretaceous belemnites, and in the 1950s she monographed the belemnites from Denmark and Greenland. Later she mainly focussed on Jurassic and Cretaceous ammonites, particularly from Greenland.

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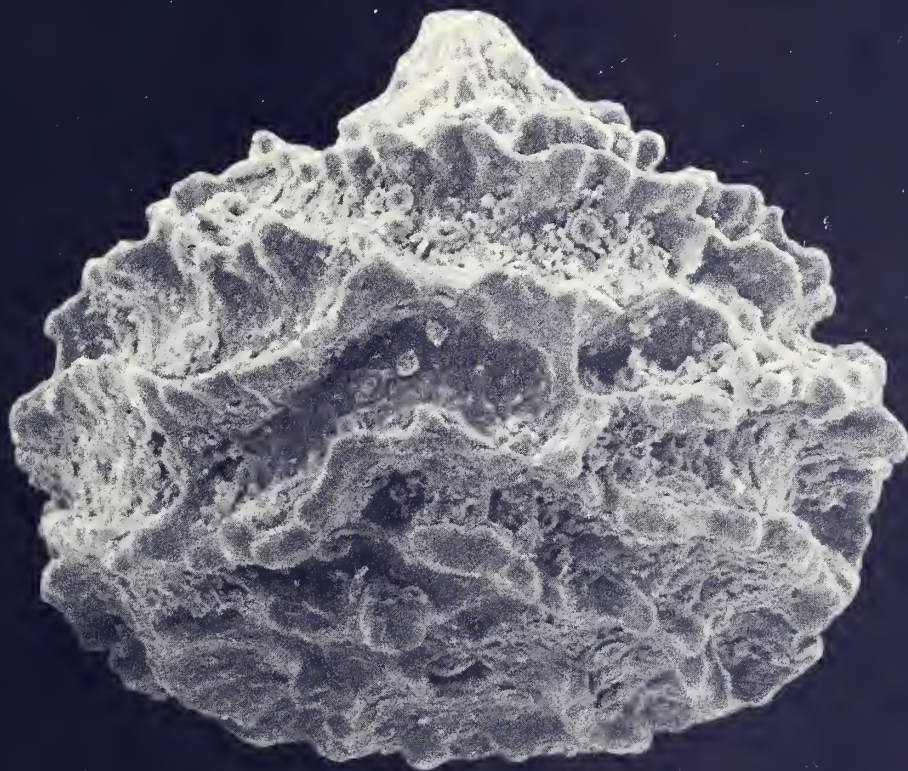
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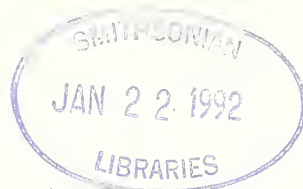
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Cover: *Bolboforma intermedia* Daniels and Spiegler (Incertae Sedis, possibly a calcified algal cyst) from Site 552A, southwest margin of Rockall Plateau, late Miocene NN9–10. $\times 800$. *Bolboforma* was planktonic and cysts are found in epicontinental shelf sea deposits, thus providing a useful biostratigraphic link with oceanic sequences.



NOVEL ULTRASTRUCTURE IN WATER- CONDUCTING CELLS OF THE LOWER DEVONIAN PLANT *SENNICAULIS HIPPOCREPIIFORMIS*

by P. KENRICK, D. EDWARDS and R. C. DALES

ABSTRACT. A description of the ultrastructure of the water-conducting cells in *Sennicaulis hippocrepiiformis* Edwards (1981), an early land plant of uncertain affinity, is based on pyrite and limonite permineralizations from two Lower Devonian localities in Dyfed and Powys, Wales. The ultrastructure of the two-layered cell wall is unique among land plants, although a simple large helical thickening suggests affinity with the Tracheophyta. The lumen of each cell is lined with a thin microporate layer that overlies the bulk of the wall, including the simple helical thickening, which has a spongy texture. Tapering end walls like those seen in tracheids have not been observed. The reconstruction of the cell wall is based on an analysis of the mineral and coalified material using polished thick sections and scanning electron microscopy; the interpretation relies on comparative morphology and recent advances in knowledge of the process of sedimentary pyrite formation. This novel cell type is shown to be very different from that recently described in a similarly preserved plant, *Gosslingia breconensis* Heard, and comparisons are also made with presumed water-conducting cells of other early land plants. The microporate layer resembles that found in some extant hepatics, although a convincing argument for a close phylogenetic relationship requires more information on the chemical structure of the wall layers and the morphology of the whole plant.

THE thirty-second annual address to the Palaeontological Association entitled 'Pioneering plants', while celebrating the variety in organization exhibited by early land plants, cautioned that preconceptions based on extant vegetation can impose restrictions on interpretation. The latter may be particularly important at a time of anatomical, biochemical and morphological innovation associated with the colonization of a new and highly stressful environment. Anticipation undoubtedly colours perception. An excellent example relates to the water-conducting tissues of land plants and, more specifically, to the tracheid or vessel which characterizes the vascular plant and which is essential to the homoiohydric condition.

Water-conducting cells of early land plant fossils have usually been interpreted as tracheids similar to those in extant plants. The presence of tracheids of apparently similar structure in different higher taxa (e.g. Rhyniophytina, Zosterophyllophytina, Trimerophytina and Lycophytina) has reinforced the concept of a monophyletic origin for these diverse groups. Recently, the identification and redescription of major cell wall features (e.g. thickening or pitting type) using scanning electron microscopy has shown that previous descriptions based on light microscope observations were often incorrect (Kenrick and Edwards 1988). Further technical refinement and a better understanding of how certain minerals form have also facilitated analysis and interpretation of cell wall ultrastructure. Thus detailed studies of the water-conducting cells ('tracheids') of the oldest well-preserved vascular plants have identified two distinctly different types of wall ultrastructure in cells that are superficially similar. The previously described *Gosslingia*-type (Kenrick and Edwards 1988) is comparable to protoxylem elements in some extant pteridophytes, whereas the *Sennicaulis*-type, described here, combines helical thickenings – a tracheid feature – with a thin microporate wall – a feature of the water-conducting cells of some hepatics.

MATERIAL AND LOCALITIES

Three sets of sterile, permineralized axes showing similar wall structure were obtained from two localities in South Wales: Mill Bay West, a new locality in Dyfed, and Brecon Beacons Quarry in Powys. Most of the material illustrated here was collected from Mill Bay (Pl. 1, figs 1, 2, 6, 7; Pl. 2, figs 1–3, 6; Text-fig. 1A, B) and contains a high proportion of limonite (see p. 758). Two illustrations (Pl. 1, figs 3 and 4) are of pyritized material from the Edwards collection of *Sennicaulis hippocrepiiformis* from Brecon Beacons Quarry and now housed in the British Museum (Natural History) – BM(NH). This material contains little or no limonite and is a good example of the type of wall structure described here as seen in polished transverse section. Further limonitic material, collected from Brecon Beacons Quarry, is used to demonstrate the helical nature of the wall thickenings because it etched well (Pl. 1, figs 6 and 7). These two localities are in separate local units of the Lower Old Red Sandstone, namely the Cosheston Group and the Senni Beds (Allen 1974; Thomas 1978).

Mill Bay West (SN 002 049). This locality on the southern shore of the Daugleddau estuary, c. 3.5 km north-east of Pembroke Dock, is in the Mill Bay Formation (Thomas 1978) of the Cosheston Group. The sequence consists of dark, grey-green, highly indurated, c. 3 m thick, interlaminated very fine-grained sandstones and coarse siltstones which have been ‘pillowed’. The pillowing is thought to be of tectonic origin and has severely deformed the bedding planes. The locality, frequently submerged at high tide, is unit 269 of Thomas (1978) and is 126 m above the base of his MBW log D. The lithology is a difficult one from which to extract plants, but has yielded abundant, sterile, coalified axes with a central strand preserved in pyrite or limonite. These new fossils have been assigned to the form genus *Sennicaulis* based on anatomical observations of the central strand.

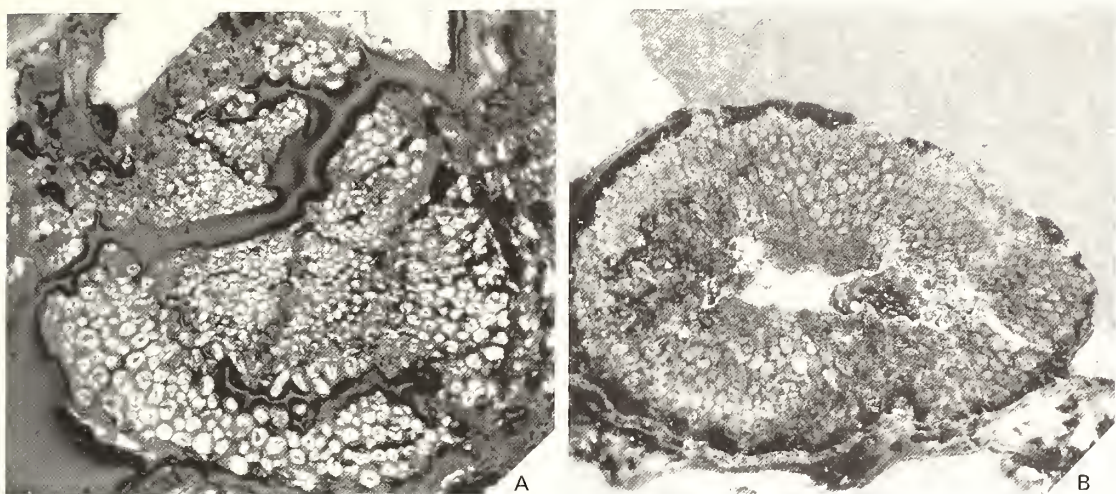
A comparative analysis of the lithostratigraphy and miospore assemblages of the Cosheston group and the Senni Beds led Thomas (1978) to equate the latter to the lower two-thirds of his Mill Bay Formation. This places the locality in the uppermost Gedinnian to lower Siegenian on palynological correlations (Richardson *et al.* 1982).

Brecon Beacons Quarry (SN 9715 2084). This is a disused roadside quarry c. 12 km south of Brecon on the main road (A470) to Merthyr Tydfil. About 14 m of the predominantly blue-grey fluvialite sediments of the Senni Beds are exposed. These consist of a series of massive sandstones (channel-fill deposits) which cut into and alternate with silty sandstones and siltstones. Some specimens assignable to *Sennicaulis*, and collected from the *Tarella trowenii* plant bed (Edwards and Kenrick 1986), contain significant amounts of limonite. One non-oxidized, pyritic specimen from the Edwards *Sennicaulis hippocrepiiformis* collection at the BM(NH) was examined. It was originally collected from plant bed 3, some 2 m above the main *Gosslingia* horizon (Friend and Williams 1978). The *Gosslingia breconensis* material illustrated here and first figured in Kenrick and Edwards (1988) was collected from horizon 4, the main *Gosslingia* plant bed (Friend and Williams 1978). Spore assemblages suggest a lowermost Siegenian age for both the *Tarella* and *Gosslingia* beds (lower part of Zone III, Richardson *et al.* 1982).

Figured specimens are housed in the National Museum of Wales, Cardiff (prefix NMW) or the British Museum (Natural History), London (prefix V).

TECHNIQUES

Specimens were examined using incident light and scanning electron microscopy. Employing these two techniques in combination enables accurate reconstructions and interpretations of the cell wall of pyritic and limonitic fossils to be made. Incident light microscopy illustrates the distribution of mineral and coalified material within the wall which is essential for interpreting the electron



TEXT-FIG. 1. A, B, *Sennicaulis hippocrepiformis*; NMW 90.42G.1; Lower Old Red Sandstone; Mill Bay West, South Wales; transverse section of xylem strand at different levels along an axis, $\times 70$; A, More or less terete strand composed of two zones of cells: inner zone of small cells surrounded by outer zone of large cells (specimen is cracked in upper left quarter). Pyrite in cell lumens (high reflectance), oxide in cell walls (low reflectance); B, elliptical shape to strand caused by collapse of outer zone cells into non-preserved middle region. Mineral is limonite.

micrographs. Scanning electron microscopy clearly illustrates the three-dimensional form of the cell and its ultrastructure.

For light microscopy, highly polished thick sections (Pl. 1; Text-fig. 1A) were made using a standard mineralogical polishing technique outlined in Kenrick and Edwards (1988). Bright field incident light microscopy produced the best results for pyritized axes and also for specimens with oxidized cell walls and pyritic lumens. Brief etching of the polished surface heightened contrast in pyritized specimens. The most effective etchant proved to be a saturated solution of ammonium ceric (IV) nitrate in dilute sulphuric acid (Biggs and Rocken 1983). The entirely limonitic specimen (Text-fig. 1B) was not polished, but saw marks were removed with 600 grit carborundum and the specimen mounted under a coverslip in Histomount and photographed using dark field illumination on an Olympus Vanox. A monochromatic green filter improved the photographic results obtained with Ilford PAN F or FP4 35 mm black-and-white film.

For scanning electron microscopy, a deep etch or a fractured surface was preferred. Concentrated solutions of nitric acid and hydrochloric acid were used to etch pyrite and limonite respectively. Etching time varied depending on the depth of etch required and the mineral present, but was typically between 5 and 15 minutes. In many instances, better results were obtained from fractured surfaces, which also served as a control for the effects of acids on wall structure in etched sections. All specimens were coated with gold and examined using a JEOL 35CS or Cambridge 360 scanning electron microscope.

SYSTEMATIC PALAEOLOGY

Edwards (1981) erected the genus *Sennicaulis* as a: 'Form genus for sterile axes, each with a prominent terete xylem strand lacking parenchyma, but for which surface characteristics and branching pattern are uncertain. Centrarch xylem composed of tracheids with annular and helical secondary thickenings surrounded by a zone of compressed thick-walled cells. Outer cortex consisting of several layers of elongate thick-walled cells. Inner cortex and epidermis not preserved.'

The specimen illustrated here (Text-fig. 1A, B) shows that the central region of these strands can be quite variable. The absence of a well-defined inner zone in Text-figure 1B, taken from the same axis as the section illustrated in Text-figure 1A, is probably due to poor preservation.

In her original description, Edwards interpreted the cell walls as being almost entirely replaced by pyrite, so no organic structure or ultrastructural features were described. Kenrick (1988) collected more material from Brecon Beacons Quarry and Mill Bay and described the wall structures illustrated here. Recently, Dales was able to confirm the presence of similar wall ultrastructure in material from the type collection. We propose, therefore, to emend the generic diagnosis, but our ignorance of the gross morphology of the plant precludes the use of any taxon above the generic level.

INCERTAE SEDIS

Genus SENNICAULIS Edwards (1981)

Type species: Sennicaulis hippocrepiformis Edwards (1981).

Original diagnosis. See Edwards (1981, p. 225).

Emended diagnosis. Form genus for sterile axes $\pm$ circular in cross section containing a prominent terete xylem strand but for which surface characteristics and branching pattern are unknown. Xylem composed of elongate elements with predominantly helical thickenings surrounding a terete central region of smaller cells. Xylem element wall two layered: a thin, continuous, microporate layer (next to cell lumen) covers a layer with spongy texture. Outer cortex consisting of several layers of elongate thick-walled cells. Inner cortex and epidermis not preserved.

Sennicaulis hippocrepiformis Edwards (1981)

Plate 1, figs 1–4, 6, 7; Plate 2, figs 1–6; Text-fig. 1A, B

1981 *Sennicaulis hippocrepiformis* Edwards, p. 225, plates 1–6, figs 1–46.

Holotype. Sections V60352–V60386; figured in Edwards (1981) pl. 1, figs 1, 3, 6; pl. 2, figs 8, 12, 13; pl. 3, figs 15 and 16; pl. 4, fig. 24; pl. 5, figs 31, 33–36; pl. 6, figs 37–44.

Paratypes. Sections V60387–V60404 and V60405–V60429; figured in Edwards (1981) pl. 2, fig. 9; pl. 3, figs 17–22; pl. 4, figs 23, 25–28; pl. 5, figs 29, 30, 32; pl. 6, fig. 45.

Type locality. Brecon Beacons Quarry, Wales (Friend and Williams 1978), Lower Old Red Sandstone (= Siegenian), Lower Devonian.

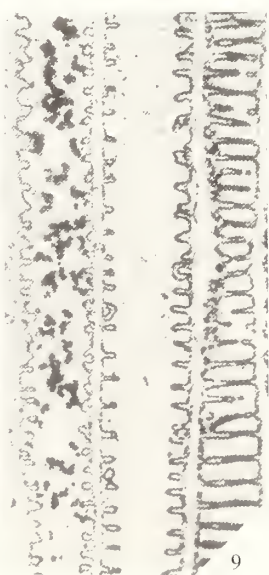
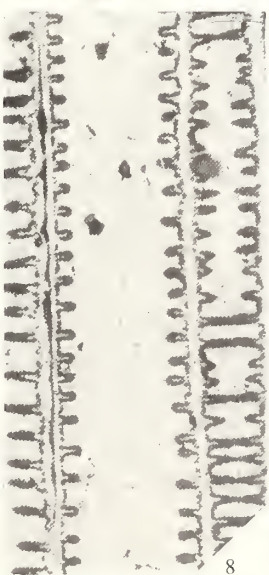
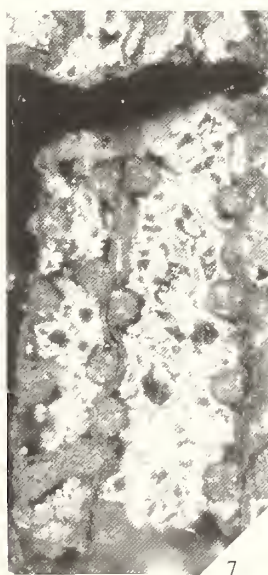
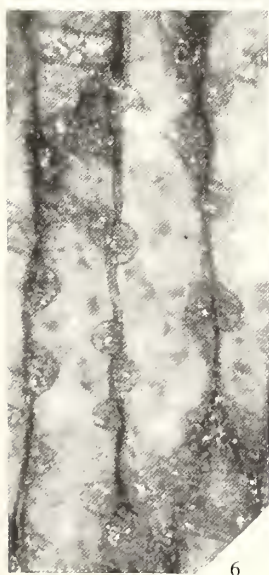
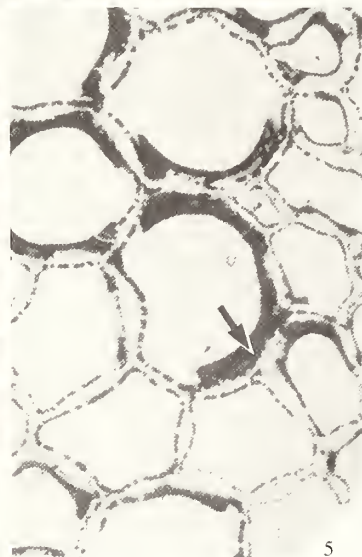
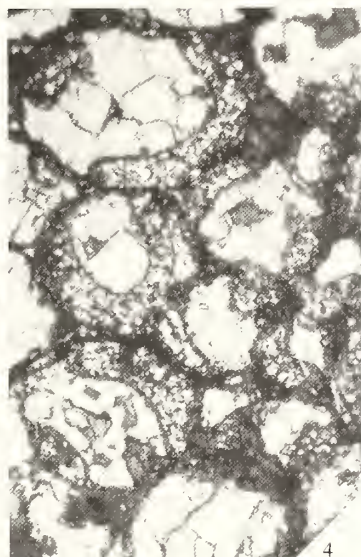
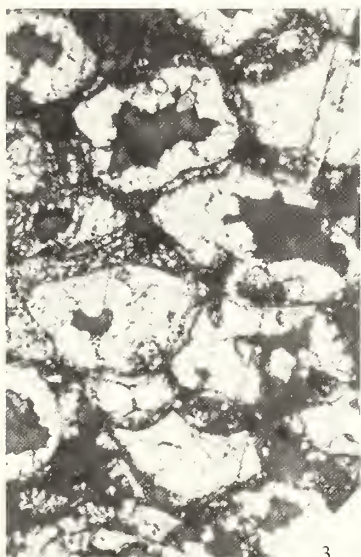
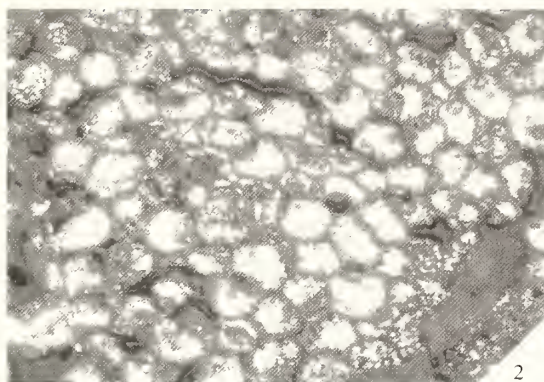
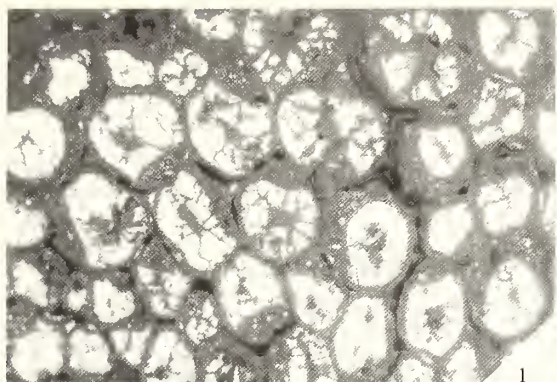
EXPLANATION OF PLATE 1

Figs 1–4. *Sennicaulis hippocrepiformis* Edwards; transverse sections (T.S.) of S-type conducting cells. 1 and 2, NMW 90.42G.1; Lower Old Red Sandstone; Mill Bay West, South Wales; outer and inner (respectively) zone cells, detail of Text-fig. 1A, pyrite cell lumina show high reflectance and limonitic cell walls low reflectance, thickenings arrowed, $\times 315$. 3 and 4, V 60388; Siegenian; Brecon Beacons Quarry, South Wales, $\times 675$.

Fig. 5. *Gosslingia breconensis* (Kenrick and Edwards); NMW 87.19G.1; Siegenian; Brecon Beacons Quarry, South Wales; T.S. of G-type xylem cell, $\times 675$.

Figs 6 and 7. *S. hippocrepiformis*; NMW 90.42G.2; Siegenian; Brecon Beacons Quarry, South Wales; longitudinal sections (L.S.) of S-type cells. 6, limonite. 7, pyrite in lumen, limonite in wall. Both $\times 510$.

Figs 8 and 9. *G. breconensis*; NMW 87.19G.2; Siegenian; Brecon Beacons Quarry, South Wales; L.S. of G-type cells preserved in pyrite, $\times 510$.



Emended diagnosis. Axes up to 6 mm diameter containing a terete xylem strand, 0.9–0.2 mm in cross-section. Xylem composed of elongate elements, with predominantly helical elements surrounding a clearly defined central region of narrower elements also helically thickened mixed with non-ornamented cells. Xylem element wall two layered: a thin continuous microporate layer (next to cell lumen) overlies a layer with a spongy texture. Micropores are 100 nm (40–200 nm) in diameter with a density of $c. 16 \mu\text{m}^{-2}$. Means and actual xylem measurements are as follows: width of thickening = $11.2 \mu\text{m}$ (6.3–27.5 μm); inter-thickening distance = $17.4 \mu\text{m}$ (5.0–32.5 μm); distance thickening protrudes into cell lumen = $9.8 \mu\text{m}$ (5.0–13.8 μm); lumen diameter at widest point = $34.5 \mu\text{m}$ (–45.0 μm); inter-thickening wall thickness $c. 2.5 \mu\text{m}$. Outer cortex composed of up to five layers of thick-walled ($c. 5 \mu\text{m}$) cells, more or less isodiametric in cross-section but decreasing in diameter and length towards the outside; mean cell width = $50 \mu\text{m}$ (25–100 μm) and cell length up to 450 μm .

DESCRIPTION OF ANATOMY

Major features of the xylem. The xylem is a more or less terete strand of elongate cells and in well preserved sections consists of two distinct zones. The outer zone is composed of large cells, up to six cells thick, and completely surrounds an inner zone of smaller cells. The boundary between the two zones is quite distinct (Pl. 1, figs 1 and 2; Text-fig. 1A). Preservation varies along a single axis and, in some regions, the central zone cells are not preserved. This appears to have resulted in collapse of the outer zone into the non-preserved central region and consequently a more elliptical outline to the strand (Text-fig. 1A).

Outer zone xylem cells. Each cell has a single large helical thickening with frequent reversals in the direction of the helix (see Table 1 for all measurements). The helical nature of the thickening is most clearly seen in etched transverse sections (Pl. 2, fig. 4); the reversal of the helix is most obvious in fractured lumen casts (Pl. 2, fig. 1). Cells are elongate, but no end walls were observed and so their total lengths are unknown. Variation in cell diameter within the outer zone suggests some tapering, but may merely indicate the presence of cells of different diameter (Pl. 2, fig. 1).

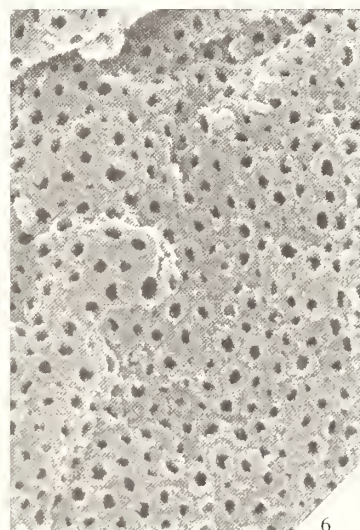
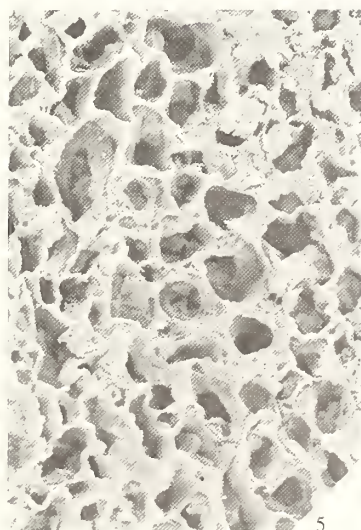
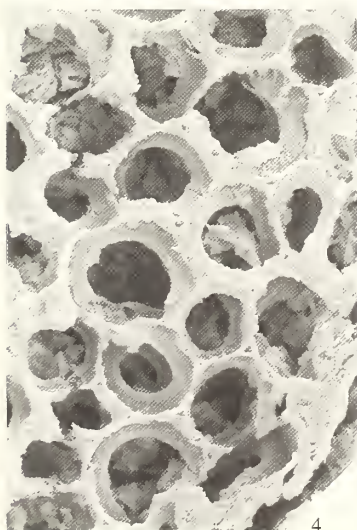
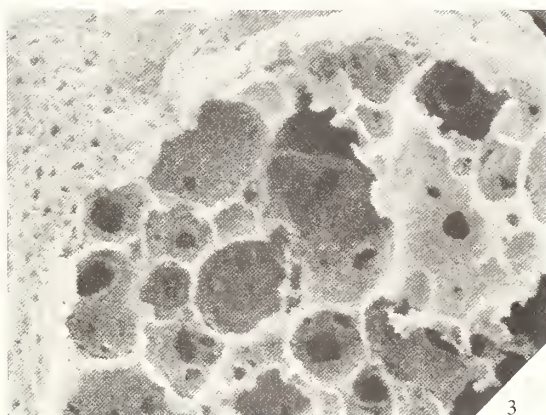
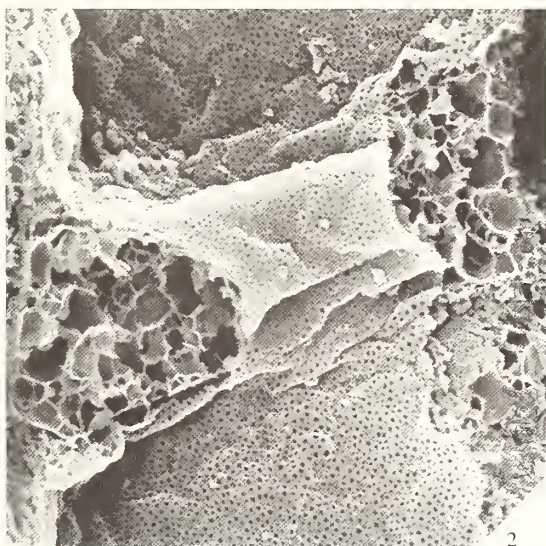
Scanning electron microscopy of fractured or etched sections shows the most ultrastructural detail (Pl. 2). At low magnification fractured sections commonly reveal lumen casts of coarse textured mineral with deep grooves marking the path of the helical thickening (Pl. 2, fig. 1: two cells on the left). Partially coalified cell walls are also present, have a smoother texture and usually retain the helical thickening itself (Pl. 2, fig. 1: two cells on the right). At higher magnification the wall is seen to consist of at least two layers: a very thin microporate layer overlies the bulk of the wall which has a spongy texture (Pl. 2, figs 2 and 3). The microporate layer is continuous over the entire inner surface of the cell and covers the thickenings as well as the wall between. Micropores, about

EXPLANATION OF PLATE 2

Scanning electron micrographs of *Semicaulis*-type (S-type) xylem cell wall structure.

Figs 1–3, 6. NMW 90.42G.3, stub 183; Lower Old Red Sandstone; Mill Bay West, South Wales. 1, fractured and partially etched longitudinal section showing lumen casts of coarse textured mineral with deep grooves marking the path of the helical thickening (two cells on left) and coalified walls where lumen casts have fallen away with thickenings arrowed (two cells on right), $\times 600$. 2, higher magnification of area in figure 1 showing structure of wall thickening: microporate wall continuous over thickening and between thickenings, $\times 3500$. 3, details of spongy interior to thickenings, $\times 12000$. 6, details of microporate wall as seen from cell lumen, $\times 14000$.

Figs 4 and 5. NMW 85.18G.27f, stub 169; Siegenian; Brecon Beacons Quarry, South Wales; details of partially demineralized thickenings in outer and inner zone cells at the same magnification, $\times 450$. 4, outer zone cells, simple helical thickenings. 5, inner zone cells, some with helical thickenings.



100 nm in diameter (ranging between 200 nm to less than 40 nm diameter), penetrate this layer completely (Pl. 2, figs 2, 3, 6). The density of micropores is approximately $16 \mu\text{m}^{-2}$. The microporate layer is very thin; its actual thickness was difficult to measure but it is estimated as approximately equal to the micropore diameter of 100 nm or less. In all cells this layer is wrinkled and this is especially noticeable on and around the thickenings themselves (Pl. 2, figs 1 and 2). It should be noted that the small size of the micropores make them difficult to resolve even at high magnification. At low magnification the inner surface of the coalified wall appears to be smooth (compare Pl. 2, figs 1 and 2).

The remainder and bulk of the wall underlying the microporate layer has a distinctive appearance that is observed most easily within the helical thickening. It is a coalified layer with a spongy texture (Pl. 2, figs 2 and 3). A thinner layer of similar composition underlies the wall layer between thickenings. There appear to be no direct connections or channels through this spongy layer connecting the micropores of adjacent cells, nor any indication of a layer separating adjacent cells.

Inner zone xylem cells. This zone consists of helically thickened cells of similar structure to those in the outer zone but also contains cells without thickenings (Pl. 2, fig. 5). Thickened cells predominate and the nature of the unthickened cells is uncertain because of the paucity of well-preserved and uncompressed material within the inner region. All cells are distinctly smaller in diameter than those in the outer zone (compare Pl. 1, figs 1 and 2).

Cellular preservation outside the xylem. There is no cellular preservation outside the xylem in specimens from Mill Bay. However, specimens from the original Edwards collection of *Semicaulis hippocrepiformis* show a narrow zone of crushed cells immediately adjacent to the xylem and a further layer of cells close to or at the edge of the axis and separated from the central tissues by a region where there is no cellular preservation. A detailed analysis of cell wall structure in these regions has not yet been undertaken.

MINERALOGICAL OBSERVATIONS

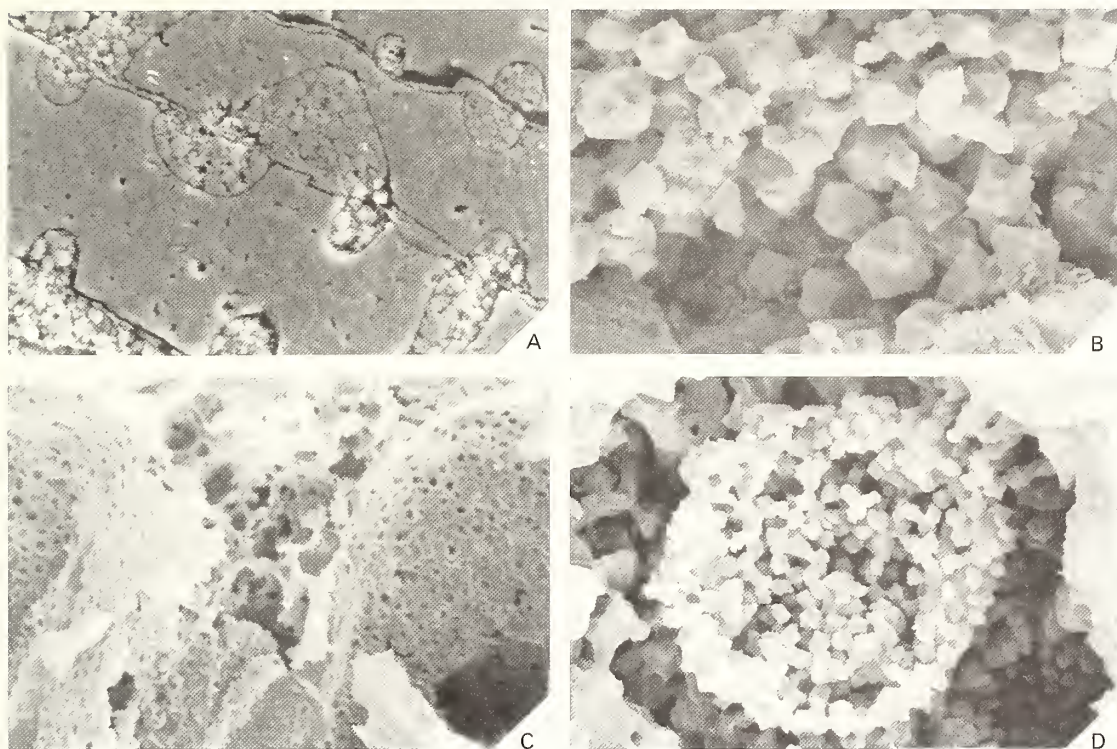
All specimens considered here are preserved in pyrite, limonite, or a combination of both minerals. Limonite is used as a broad term that can encompass virtually any combination of the various iron oxides and hydroxides that exist naturally. In fossil plants it forms by the oxidation of pyrite and pseudomorphs pyrite textural morphologies. The timing of this oxidation cannot be defined more specifically than post pyrite formation.

Observation of polished thick sections in reflected light clearly shows the distribution of mineral and coalified material in the wall of pyritized specimens (Pl. 1, figs 3 and 4), in that pyrite has high reflectance and the coalified material has low reflectance, although precise identification of coaly material in such sections remains a problem (Kenrick and Edwards 1988). While other non-opaque minerals (e.g. silicates) have a similar low reflectance, we interpret the spongy structure in the composite wall as organically derived, because it is acid resistant, has no discernible crystalline structure and is similar in composition and structure in all modes of permineralization in all occurrences. At very high magnifications both microporate and spongy material show a similar texture, which is not observed elsewhere in the permineralized cells.

Pyrite textures

Considering those in the lumen of the tracheid, pyrite textures can be divided into three morphologies.

Equant euhedra of pyrite. These have an average grain size of 4–10 μm and are surrounded by a later overgrowth of pyrite. In transverse section 2–6 euhedra are visible in each cell lumen, while in longitudinal section many tens of euhedra were seen (Text-fig. 2A, B). Equant euhedra were also observed within the coalified helical thickenings (Text-fig. 2A).



TEXT-FIG. 2. Pyrite textures observed within the xylem of longitudinally fractured axes of *Semicaulis hippocrepiformis* from the Brecon Beacons Quarry, South Wales. A, V 60402; sections through pyrite euhedra in the helical thickenings following light etch, $\times 1800$. B, V 60402; euhedra within lumen: in such a deeply etched longitudinal section individual euhedra show their distinctive octohedral form, $\times 2000$. C, V 60415; strongly etched axis with helical thickenings (cf. Pl. 2, fig. 3) in which voids left by the removal of pyrite show little resemblance to the octohedral pyrite morphology, and are thought to be related to the original structure of the wall, $\times 8280$. D, V 60415; framboid within lumen of tracheid: individual crystallites $\geq 1 \mu\text{m}$ cluster to form framboids $10\text{--}20 \mu\text{m}$ diameter, $\times 3450$.

Framboidal pyrite. Framboids (Text-fig. 2D) are often surrounded by a later overgrowth or overgrowths of pyrite and are less common than in analogous areas of lumen in *Gosslingia breconensis* (Kenrick and Edwards 1988).

Bladed pyrite. Some pyrite crystals extend from points on or adjacent to the cell wall out into the cell lumen (Pl. 1, figs 1–4). Sometimes pyrite infilling of the cell lumen is incomplete, leaving a space which may be filled later with another diagenetic mineral, typically calcite (Pl. 1, figs 1–4).

The helical thickenings are filled with euhedra of pyrite (*c.* $2\text{--}4 \mu\text{m}$) within what is interpreted as a coalified 'spongy' matrix. The high reflectance of the pyrite and the low reflectance of the coalified material give the 'C'-shaped thickenings a speckled appearance in polished section (Pl. 1, fig. 4, Text-fig. 2B).

In specimens that are partially pyritic and partially limonitic (Pl. 1, figs 1, 2, 7; Text-fig. 1A) particular care must be taken when interpreting the extent of the mineralization of the cell wall. Limonite formation in fossil plants generally seems to start within the cell wall and may or may not proceed to the pyrite of the lumen (Kenrick 1988). We suggest that the microcrystalline pyrite and

organic material within the wall provide a relatively easy route into the specimen for oxidizing chemicals. In contrast, the large pyrite crystals and paucity of coalified material within the cell lumen prove a more effective barrier to oxidation. Oxidation produces a mineral with reflectance similar to that of the coalified material but much lower than that of pyrite. This makes it difficult to assess the relative abundance and distribution of mineral within the cell wall of partially oxidized specimens using reflectance alone. Superficial examination may erroneously suggest (Pl. 1, figs 1, 2, 7) that the walls are heavily, or almost entirely, coalified.

Specimens in which most or all of the pyrite has been oxidized are better viewed in dark field illumination (Pl. 1, fig. 6; Text-fig. 1B). Although major wall features such as thickenings are easy to see, lack of contrast makes it difficult to assess the distribution of mineral and coalified material.

TAPHONOMY

The description and interpretation of wall features in *Sennicaulis* in terms of original cell wall structures requires an understanding of taphonomic processes and an analysis of the effects of pyrite formation on cell wall structure. The process of sedimentary pyrite formation in recent sediments is relatively well understood (Berner 1984), and the way this process affects the appearance of the plant cell wall has been discussed at length by Kenrick and Edwards (1988) in relation to another Lower Devonian plant, *Gosslingia breconensis*.

The pyritization process in fossil plants is seen as one of selective decay by a consortium of bacteria ending with sulphate reducers and replacement by iron monosulphides which are eventually converted to pyrite. Decay of the fossil plant is selective because some tissue systems are less resistant to bacterial decomposition or more attractive in terms of energy yield than others. For example, woody tissue is persistent in the fossil record because of the decay-resistant lignin component within the cell wall, whereas thin-walled, non-lignified parenchyma is comparatively rarely preserved. Easily decomposed tissues may be entirely replaced by pyrite, whereas woody tissues often retain their original form although the organic material within the cell wall has been diagenetically altered. This argument has been extended to explain the distribution of pyrite and coalified material *within* a cell wall (Kenrick and Edwards 1988). For example, within the xylem cell walls of *Gosslingia breconensis* mineral and coalified material are distributed in a characteristic and consistent pattern. The most plausible explanation for this is that the distribution of coalified material faithfully reflects the pattern of decay resistant chemicals within the wall (usually identified as lignin) and the distribution of pyrite reflects the pattern of decay within the wall (i.e. the middle lamella and areas of cellulose with little or no aromatic components).

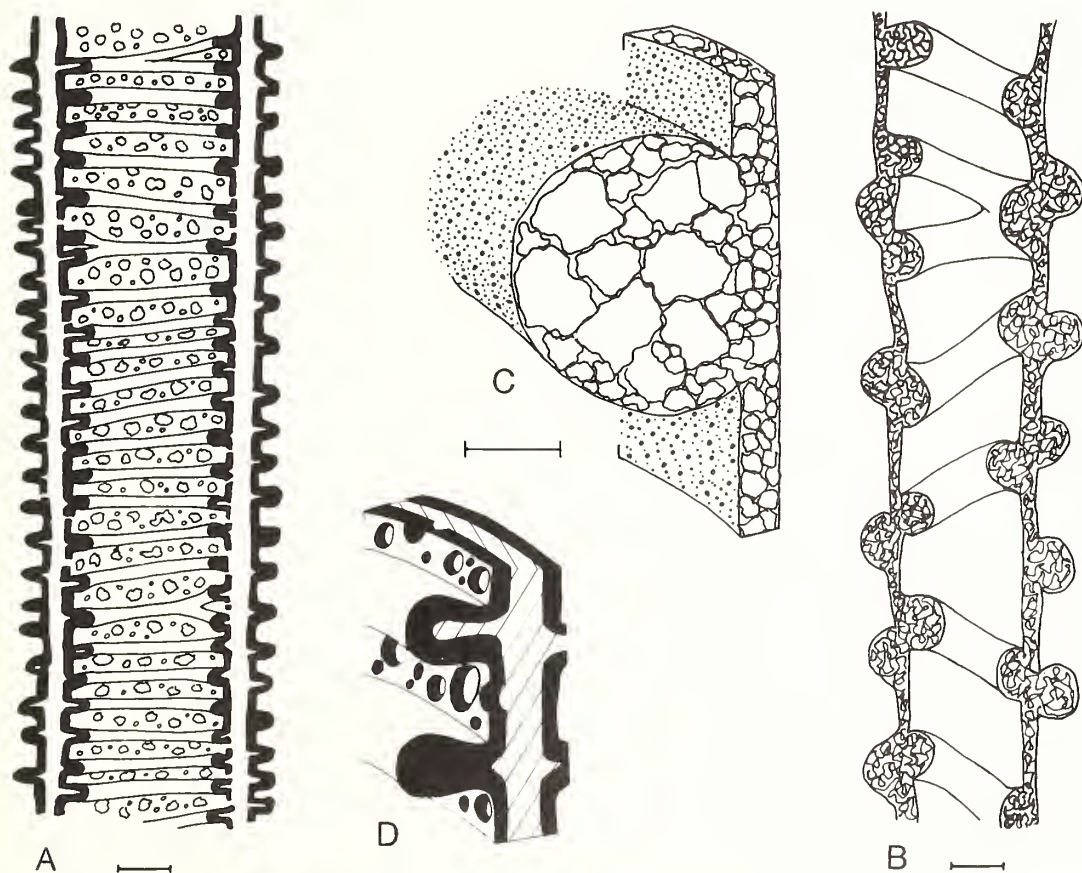
Mineral and coalified material are also distributed in a characteristic and consistent pattern in the cell wall of *Sennicaulis*, although in a different manner to that found in *Gosslingia*. Since there is little or no cellular preservation outside the xylem strand, the perforate coalified layer and the underlying spongy coalified material must be relatively decay resistant and therefore are interpreted as having an aromatic non-polysaccharide component. The microporate layer is of uniform composition and, by comparison to walls of similar outward appearance in the water-conducting cells of the Hepaticae, may be plasmodesmata derived, although their presence in the region of the thickenings is difficult to explain (see p. 764). The micropores are not preservation effects caused by microcrystalline pyrite growth because: (1) pyrite crystals of this size have not been observed in the cell wall, (2) the pores are not angular in outline as is the cubic crystal structure of the mineral, (3) the abundant larger pyrite crystals do not damage this layer, and (4) the feature is regular and uniform in plants from different localities. We also do not consider that the pores were produced during etching procedures as they are also present in fractured specimens. The wrinkling and thinness of the microporate layer suggests that, although resilient, its primary role was not structural. The underlying spongy layer that forms the bulk of the wall both within and between thickenings is more difficult to interpret. That it is decay resistant is evident; whether there was an entirely polysaccharide component occupying the cavities in the spongy texture or whether those cavities were water or air-filled features of the wall is difficult to assess. It seems unlikely that the

spongy texture is an artefact caused by pyrite crystal growth within the cell wall because the shape of the cavities does not mirror the cubic crystal structure of the mineral.

TERMINOLOGY AND COMPARISONS OF CONDUCTING ELEMENTS

We propose the terms 'S-type' and 'G-type' for the types of wall thickening and composition in two distinctive early land plant water-conducting cells (Text-fig. 3).

The 'S-type' as exemplified by *Sennicaulis* is an elongate cell with a large, simple helical thickening (*sensu* Bierhorst 1960). The wall is two layered: a thin, continuous, coalified, microporate inner layer (next to the cell lumen) overlies a thick coalified spongy layer forming most of the



TEXT-FIG 3. Diagrammatic representation of G-type (*Gosslingia*) (A, D) and S-type (*Sennicaulis*) (B, C) cells and cell walls. A, B, longitudinal sections through G-type and S-type cells at the same magnification, showing in face view the shape, size and density of the thickenings; scale bar = 10 μm ; A, G-type note the discontinuous nature of the inner wall layer (i.e. that part of the wall facing the lumen); B, S-type note the continuous wall over and between thickenings. C, D, S-type and G-type cell walls in section at the same magnification; scale bar = 2 μm ; C, S-type showing two layered wall the bulk of which is made from a spongy material underlain by the very thin microporate wall (stippled). Stippling indicates size and density of micropores on surface and is not for purposes of shading; D, G-type showing two layered wall: an inner decay-resistant layer (black in section, white on the surface) and an outer layer not resistant to decay often also found inside thickenings (shaded with diagonal lines).

interior of the thickening and the wall between thickenings. The coalified remains represent relatively decay resistant material within the cell wall, but their distinctive form and distribution are unlike that seen in the lignified walls of tracheids. Since we can find no comparable structures in tracheids of extant plants, except for the helical thickening, we consider it unwise to go further and interpret the original chemical composition of the decay resistant component as 'lignin', although presumably it is of an aromatic nature.

The 'G-type' is typified by *Gosslingia breconensis* (Kenrick and Edwards 1988) and has indirectly attached annular or tilted annular thickenings (*sensu* Bierhorst 1960). In fossils the indirect attachments are in the form of perforated sheets of coalified material between adjacent annular bars. Some elements also have direct attachment between adjacent annular bars (*sensu* Bierhorst 1960). In pyrite permineralizations the wall is clearly two layered: a relatively thick discontinuous coalified layer overlies one replaced by pyrite. The distribution of pyrite reflects the distribution of decay resistant chemicals within the cell wall (Kenrick and Edwards 1988) and since this pattern in the G-type is similar to that in the tracheids of some extant plants, we tentatively interpret the chemical composition of the decay resistant component as 'lignin', and the pyritized one as predominantly cellulose.

In polished longitudinal section both types of cell appear superficially similar as it is impossible to distinguish unequivocally between helical and tilted annular thickenings. However, direct comparison at the same magnification shows several obvious differences in the size, shape and distribution of thickenings (compare S-type element in Plate 1, figs 6 and 7, with G-type element in Plate 1, figs 8 and 9; Table 1). The S-type elements have larger thickenings that are more rounded and widely spaced, even though cell lumen diameters in both types of cell are very similar. Taking mean values, thickenings in the S-type element are three times as large and six times further apart than those in G-type elements of comparable lumen diameter. An interesting result is that in cells of comparable maximum lumen diameter, the effective diameter for fluid conductance (Jeje and Zimmermann 1979) in the S-type cell is just over half what it is in the G-type (Table 1). This is most noticeable in transverse sections of similar magnification viewed side by side (compare S-type element in Plate 1, fig. 4 with G-type element in Plate 1, fig. 5; Table 1).

TABLE 1. Comparative measurements of cell wall dimensions for S-type and G-type cells. For fuller explanation of δ , Σ , t , W , D and TW see Kenrick and Edwards (1988). δ = width of thickening; Σ = interthickening distance; t = distance thickening protrudes into cell lumen; W = maximum lumen diameter; D = effective diameter for fluid conductance; TW = thickness of wall. MBW = Mill Bay West, BBQ = Brecon Beacon Quarry, N = number of measurements.

Element type	Locality		δ	Σ	t	W	D	TW
S-type	MBW	mean μm	11.2	17.4	9.8	34.5	14.9	2.5
		max. μm	27.5	32.5	13.8	45.0	17.4	—
		min. μm	6.3	5.0	5.0	—	—	—
		N	74	77	52	11	—	—
G-type	BBQ	mean μm	3.3	2.8	3.6	29.6	22.4	—
		max. μm	4.5	5.3	6.1	50.0	37.8	3.5
		min. μm	1.5	1.0	1.5	—	—	1.5
		N	36	33	16	23	—	—

Only helical thickenings were observed in the S-type element (clearly seen in scanning electron micrographs of etched sections, Pl. 2, fig. 4). The frequent reversal in direction of the helix in the S-type cell (Pl. 2, fig. 1) has also not been seen in the G-type. Both annular and helical thickenings clearly occur in the G-type element along with frequent direct connections between adjacent annular bars.

Ultrastructural differences are still more marked (Text-fig. 3). Both types of cell have a wall of at least two layers although whether or not homologous is debatable. In the S-type cell, the inner part of the wall is preserved as a very thin, coalified, microporate layer that is continuous over the entire inner surface of the cell. In the G-type cell, the inner part of the wall is relatively thick and continuous over the inner surface of the cell except for relatively large holes of variable size between thickenings (see Text-fig. 3). Unlike the micropores in the S-type element, these holes never occur on the thickenings themselves. The micropores of the S-type element are about 100 nm diameter (ranging from 200 nm to less than 40 nm) with a density of about $16 \mu\text{m}^{-2}$, whereas the holes in the G-type measure about 2–3 μm diameter (ranging from 4 μm to about 0.5 μm).

The second layer or outer part of the wall in the G-type element which is entirely pyritized in *Gosslingia* is approximately the same thickness as the inner. In contrast, the outer layer of the S-type element forms the bulk of the wall and although partially pyritized contains a significant proportion of structured coalified material (Text-fig. 2c).

DISTRIBUTION OF S- AND G-TYPES

S-type

There is only one other fossil plant in which ultrastructural features comparable to those in the S-type element have been described. Hueber (1982) described helically strengthened tubes in axes assignable to *Taeniocrada dubia*. He observed three components in the structure of the wall: 'an outer, thin, fibrillar layer; sponge-textured helical thickenings; and a microporate layer that lines the lumen of the tube'. Apart from the outer, thin, fibrillar layer which has not been observed in S-type elements from *Sennicaulis* the structure of the wall would appear to be identical although no photographs of Hueber's material have yet been published. The conducting strand is described as centrarch in *T. dubia* but in *Sennicaulis* from the Mill Bay locality it is clearly divided into two distinct zones, at least over part of the axis. The inner zone is often not well preserved and in many sections is totally missing. When this occurs, the outer zone cells collapse inward and this, combined with the presence of crushed cells in the centre, may give the impression of a centrarch strand.

Few ultrastructural studies have been performed on early land plant water-conducting cells so it is impossible to identify unequivocally other plants with similar wall structure. However, the shape and size of the helical thickenings in the S-type cell are strikingly different from those in the G-type (see Table 1 and p. 761) and may prove to be characteristic. The recent reinvestigation of *Stockmansella langii* (formerly *Taeniocrada langii*) illustrates cells with certain similarities to the S-type (Fairon-Demaret 1985, 1986), although organic material in the cell wall could not be recognized. Fairon-Demaret (1985) noted that the spacing and tilt of the thickenings, seen as grooves on goethite casts of the cell lumen, indicate a simple helical thickening with frequent inversions in the tilt, and that in this feature these cells are similar to those of *Rhynia gwynne-vaughanii*. These features, together with the dimensions of the thickening, point to a structure similar to that in the S-type cell.

Edwards (1981) and Edwards, D. S. (1986) have both commented on the similarities between the helical elements of *Sennicaulis hippocrepiformis* and *Rhynia gwynne-vaughanii*, including the size and shape of thickenings, originally described as annular in *R. gwynne-vaughanii* (Kidston and Lang 1917), and the frequent reversal of the helix within cells, all typical features of the S-type element. Edwards D. S. (1986) was unable to find an organic wall in etched tracheids of *R. gwynne-vaughanii*, so the wall ultrastructure is unknown. The xylem strand of *R. gwynne-vaughanii* is also much smaller than that illustrated here and is not divided into distinct zones.

There are no known examples of S-type conducting cells among extant vascular plants. Helical elements are common in the protoxylem, but lignin never forms in a continuous sheet on the inner surface of the cell, nor are there micropores comparable to those illustrated here.

Although the microporate layer is unknown in tracheids, a wall of similar appearance, but lacking helical thickenings and, presumably, decay resistant aromatics, is sometimes found in bryophyte

gametophytes (Héban 1979). In certain Hepaticae, as well as the enigmatic genus *Takakia*, the presumed cellulose walls of water-conducting cells have numerous plasmodesmata-derived perforations of similar size and density to those found in *Sennicaulis*. (Compare Plate 2, figures 2 and 6 with Héban's (1979) figure 2.) The whole wall thickness of these cells is similar to the thickness of the microporate layer in the S-type element. Such a microporate wall is not found in the hydroids of mosses (Héban 1979).

G-type

A review of the distribution of G-type elements was given by Kenrick and Edwards (1988). Earlier reports of scalariform or reticulate pitting in zosterophylls have been shown to be incorrect in all instances where scanning electron microscopy has been undertaken. Instead, G-type elements with annular or helical thickenings characterize the metaxylem of zosterophylls, Barinophytales and a group of fossil plants (*Asteroxylon*, *Baragwanathia* and *Drepanophycus*) similar in vegetative characteristics to modern herbaceous lycopods. With one exception (*Leclercqia*, Grierson 1976), the protoxylem elements of those and other important Devonian taxa have not received the same detailed consideration as the metaxylem and are described as helical or annular.

GENERAL DISCUSSION

In our studies of *Gosslingia* tracheids we were able to interpret their wall structure in terms of that in extant tracheids, although examples are rare. In addition it is possible that the perforate sheet in the G-type element is homologous with the pits of trimerophytes where there are perforated sheets of secondary wall material within the pit chamber (Hartman and Banks 1980) and possibly even with strands of secondary wall material in the pits of Carboniferous lycopods.

In contrast to all these taxa, the gross morphology of the plants that produced S-type cells is poorly understood and the structure cannot be directly related to other presumed water-conducting cells. Compression fossils of *Sennicaulis hippocrepiformis* from Brecon Beacons Quarry are unknown but permineralizations suggest that the axes were more or less terete in cross section. The Mill Bay West anatomy was obtained from compressions of long, ribbon-like, sterile axes. The Gaspé (Quebec) specimens of *Taeniocrada dubia*, which show a similar cell-wall structure, were originally described by Dawson as the rhizomata of *Psilophyton princeps* (Hueber 1967, 1982). Hueber (1982) described the plant as ribbon-like, with a thin cuticle and stomata. Reproductive parts were not found on specimens from which he isolated anatomy, although terminal sporangial trusses have been described from German material (Høeg 1967; Kräusel and Weyland 1930).

Gross morphology is better understood in *Stockmansella langii* (Fairon-Demaret 1985, 1986) and *Rhynia gwynne-vaughanii* (Edwards D. S. 1986), taxa united by sporangial abscission. Ultrastructural wall features have not been described for either plant and are currently under investigation.

The novel wall structure in the water-conducting cells of *Sennicaulis* and *Taeniocrada* cannot easily be compared with that in extant tracheids nor indeed with hydroids in mosses. The cell is superficially similar to an early formed protoxylem tracheid in that it has a helical thickening, but the wall layers are unlike those in the tracheids of extant plants and the more tracheid-like cells of some early land plant fossils. Terms such as primary and secondary wall are difficult to apply and have been avoided. The micropores are probably developmentally similar to the plasmodesmata derived pores in the water-conducting cells of some hepatics and functionally similar, at least in the wall layer between thickenings, but their presence in the layer over the latter is more difficult to interpret developmentally. The cell might be considered plesiomorphic in this respect.

Reinvestigation of the cell walls of the xylem of *Rhynia major*, now *Aglaophyton major*, showed that there are no internal thickenings and that the plant does not have tracheids (D. S. Edwards 1986). This was a surprising find in one of the two species of a genus that has come to represent the archetypal early vascular plant, and demonstrates that branched sporophytes do not imply vascular plant status. Our investigation shows that helical thickenings in water-conducting cells do not imply

a tracheid-like wall structure. In the case of *Semicaulis*, ultrastructural studies were required to demonstrate the novel organization. Many early land plant fossils of the rhyniophyte grade are included in Tracheophyta because of helical or annular thickenings in the xylem cells. The systematic position of these fossils must be re-evaluated because in most cases detailed studies of water-conducting cells have not been undertaken. It is natural to go further and question whether 'tracheid' can be used as a synapomorphy for vascular plants and to speculate on the relationships of plants with S-type cells. For the moment we do not wish to go beyond the recognition of a level of organization that would seem to fall between that of the extant bryophytes and vascular plants. More information is required on the morphology of plants with S-type cells and an exhaustive phylogenetic analysis is necessary before explicit statements of relationships can be made.

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THE PANGAEA DICYNODONT *RECHNISAUROS* AND THE COMPARATIVE BIOSTRATIGRAPHY OF TRIASSIC DICYNODONT FAUNAS

by C. BARRY COX

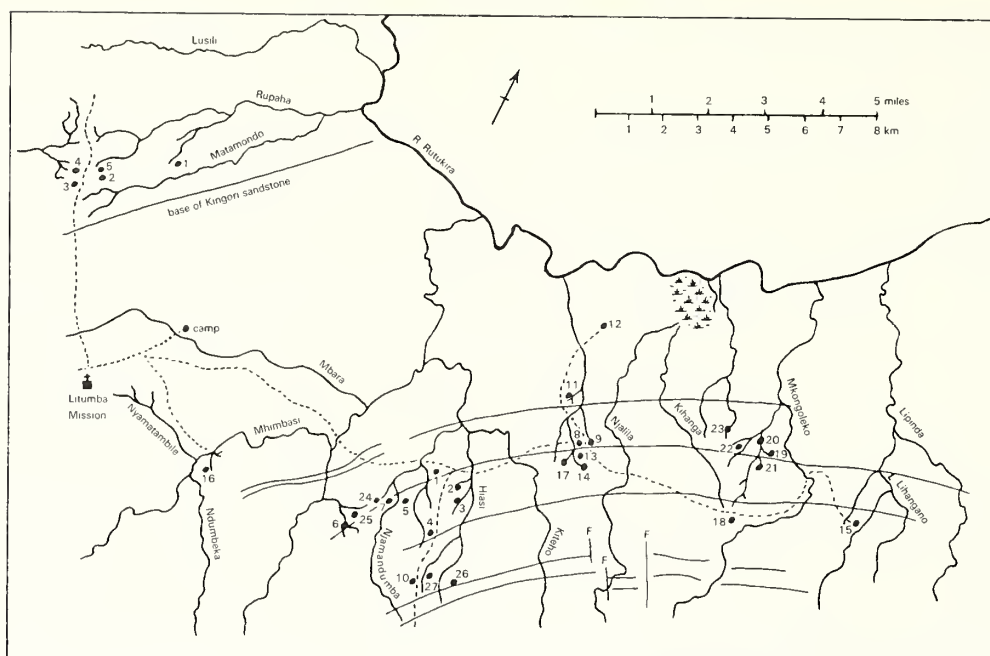
ABSTRACT. A dicynodont from the Triassic Manda Beds of East Africa is found to belong to the kannemeyeriid genus *Rechnisaurus*, first described from India, with which the genus *Shaanbeikannemeyeria* from China and Mongolia is congeneric. The divergent skull modifications of the Families Lystrosauridae and Kannemeyeriidae from the primitive Permian dicynodont skull morphology are explained in functional terms, both being adaptations to increase the length of the jaw adductor muscles. The kannemeyeriid pattern is similar to that of the ceratopsian dinosaurs, while that of the lystrosaurids seems also to be the result of feeding adaptations rather than suggesting semi-aquatic life. The relative ages of dicynodont-bearing Triassic faunas are reviewed in the light of recent changes in taxonomy and biostratigraphy.

THE Triassic Manda Beds of Tanzania were discovered by Stockley in 1930 (Stockley 1932), and his fossils were described by Haughton (1932). Further collections were made by both Parrington and Nowack in the 1930s. Study of this material showed that the fauna contained a large amphibian, the rhynchosaur *Stenaulorhynchus*, thecodontians, cynodonts, and dicynodonts (Haughton 1932; Huene 1938*a*, 1938*b*, 1942, 1950; Parrington 1946; Crompton 1955; Cruickshank 1965, 1967, 1986; Cox and Li 1983).

The British Museum (Natural History) and London University Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika spent six weeks collecting in the Manda Formation in 1963 (Attridge *et al.* 1964), and 184 specimens of dicynodonts, cynodonts, rhynchosaurs, and thecodontians were collected from 27 localities. These localities are shown on the accompanying map (Text-fig. 1), which is based on a mosaic of aerial photographs and on survey work by the late Dr W. W. Bishop (then Curator of the Uganda Museum). Local villagers provided the names of the streams.

Bishop (1968) described the geology of the area. The Manda Formation is 2000 m thick, being a series of purple to chocolate-coloured mudstones interbedded with grey to whitish sandstones and grits of variable thickness and persistence. Though reptile bones were found from 150 m above the base of the Formation to 60 m below its top, 65% of the specimens collected were found in two levels, 1180 m and 1310 m above its base. Below the Manda Formation lies the 700 m thick Kingori Sandstone Formation, from which Cruickshank (1986) reports the dicynodont *Kannemeyeria*. Below the Kingori Sandstone lies the 275 m thick Kawinga Formation, and the base of the exposed sequence in the area is made up of the 535 m thick Ruhuhu Formation, in which the 1963 Expedition found a few specimens of endothiodont dicynodonts, some of which bore canine teeth lateral to the main maxillary tooth-row.

The dicynodont *Angonisaurus* from locality 12 in the Manda Formation has already been described (Cox and Li 1983). The present paper is concerned with a large dicynodont from this formation, and with its implications for the structure, classification, and comparative stratigraphy of Triassic dicynodonts.



TEXT-FIG. 1. Map of the main collecting areas of the 1963 Expedition in the Ruhuhu Valley, south-western Tanzania. Localities (numbered) to the south lie in the Triassic Manda Formation, those to the north-west lie in the Late Permian Ruhuhu Formation. Curving lines indicate the locations of resistant levels in the Manda Formation, which caused low ridges in the landscape. Dashed lines indicate footpaths.

SYSTEMATIC PALAEONTOLOGY

Suborder ANOMODONTIA Owen, 1859

Infraorder DICYNODONTIA Owen, 1859

Family KANNEMEYERIIDAE Huene, 1948

Genus RECHNISAUROS Chowdhury, 1970

1980 *Shaanbeikannemeyeria* Cheng, p. 139, text-figs 29–30.

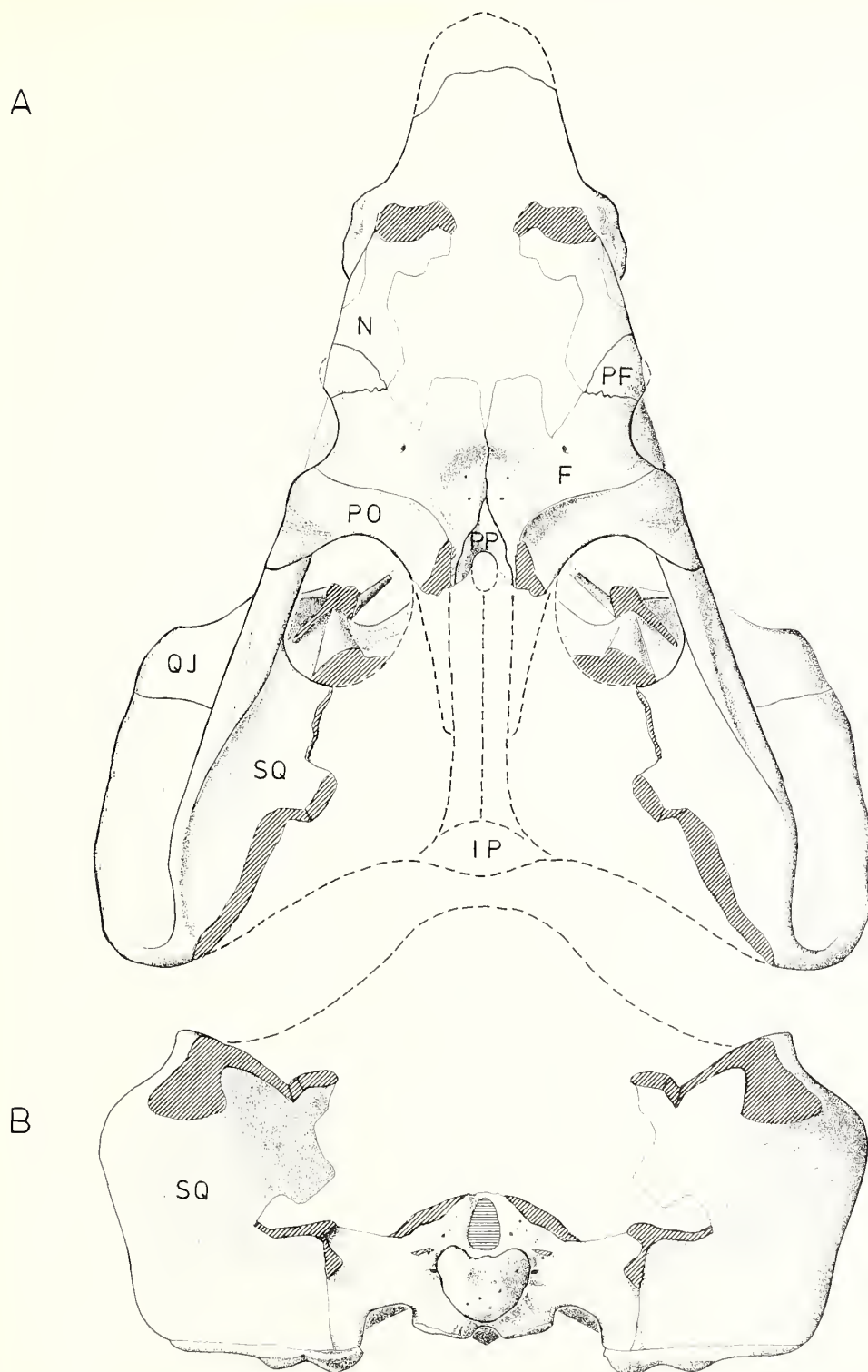
Diagnosis. Large dicynodont: skull 400–650 mm long. Skull tapers anteriorly from wide posterior squamosal region to rather narrow, blunt snout. Median ridge on premaxillae and nasals. Maxillary tusk emerges from inner side of caniniform process; no other teeth. Caniniform process of maxilla antero-ventrally directed, its posterior margin flared laterally, rugose. Interorbital bar at sharp angle to interorbital bar, rather narrow but transversely concave, lacking median crest. Wide lateral wings of squamosal directed sharply antero-ventrally, almost parallel to zygomatic arch. Quadrate lies far forward. Very short median pterygoid meeting behind short interpterygoid vacuity. Processus cultriformis of parasphenoid projects strongly antero-dorsally.

Type species. *Rechmisaurus cristarhynchus* Chowdhury, 1970.

Rechmisaurus cristarhynchus Chowdhury, 1970

Text-figs 2 and 3

Material. The specimen described here, R11955 in the Natural History Museum, field no. U17/1, was collected from locality 17 (Text-fig. 1), nearly 14 km from the Lutumba Mission Station, Songea District, south-western



TEXT-FIG. 2. *Rechinisaurus cristarhynchus*; BM(NH) R11955, $\times 0.2$. A, dorsal view, at right angles to interorbital area. B, occipital view. For abbreviations see Text-figure 3.

Tanzania, from the lower of the two main fossiliferous levels of the Manda Formation. Much of the skull was found lying on its ventral surface on the top of a low sandstone hillock. Many fragments of the dorsal surface had already been weathered off and had rolled down the sides of the hillock. They were found scattered over an area of a few hundred square metres.

Description. The whole of the snout anterior to the caniniform processes of the maxillae is missing, as is the dorso-median part of the snout as far back as the level of the front of the orbits, and the whole of the dorso-median part of the skull posterior to the pineal foramen and dorsal to the foramen magnum.

In dorsal view (Text-fig. 2A), the skull is 570 mm broad across the occiput, and tapers anteriorly. The preserved part of the skull is 590 mm long, but the original length was probably about 650 mm. The interorbital region is broad. There is a depression in the postero-median region of the frontals, behind which the bone rises steeply to form the beginning of a high intertemporal bar. The lateral walls of the depression are formed by ridges which mark the junction of the postorbital and frontal, and which curve antero-laterally, dying out towards the root of the post-orbital bar. There is no trace of a postfrontal bone. The preparietal forms the lateral and anterior walls of the pineal foramen, and tapers anteriorly to a sharp point projecting between the frontals.

The lateral walls of the pineal foramen diverge posteriorly, suggesting that these surfaces extended posteriorly as the inner surfaces of a pair of ridges along the intertemporal bar, which would then have had a median groove. The width of the posterior end of the postorbital bone, which extends laterally as a wing from the more median bones, suggests that the anterior part, at least, of the intertemporal bar, was quite wide. The ventral surface of the posterior ends of the postorbital bones are at a sharp angle to the interorbital region, indicating that the intertemporal bar rose abruptly postero-dorsally.

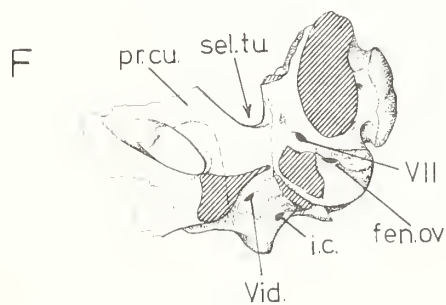
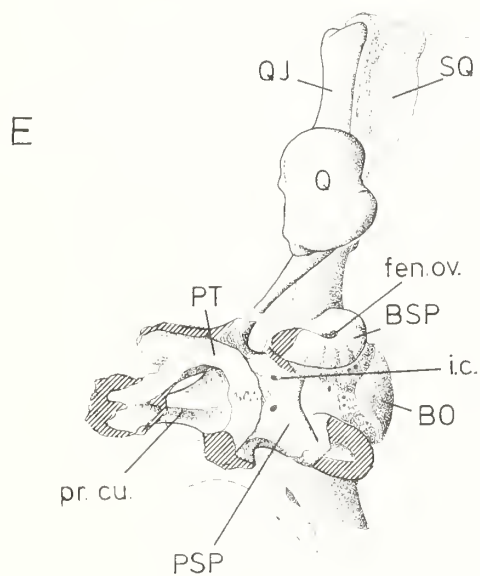
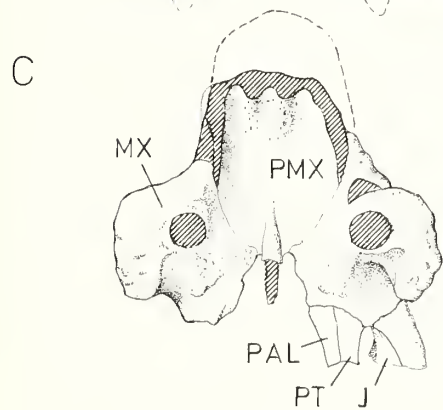
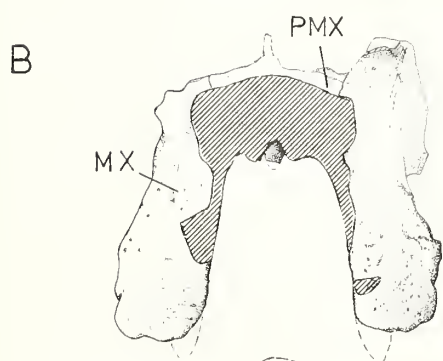
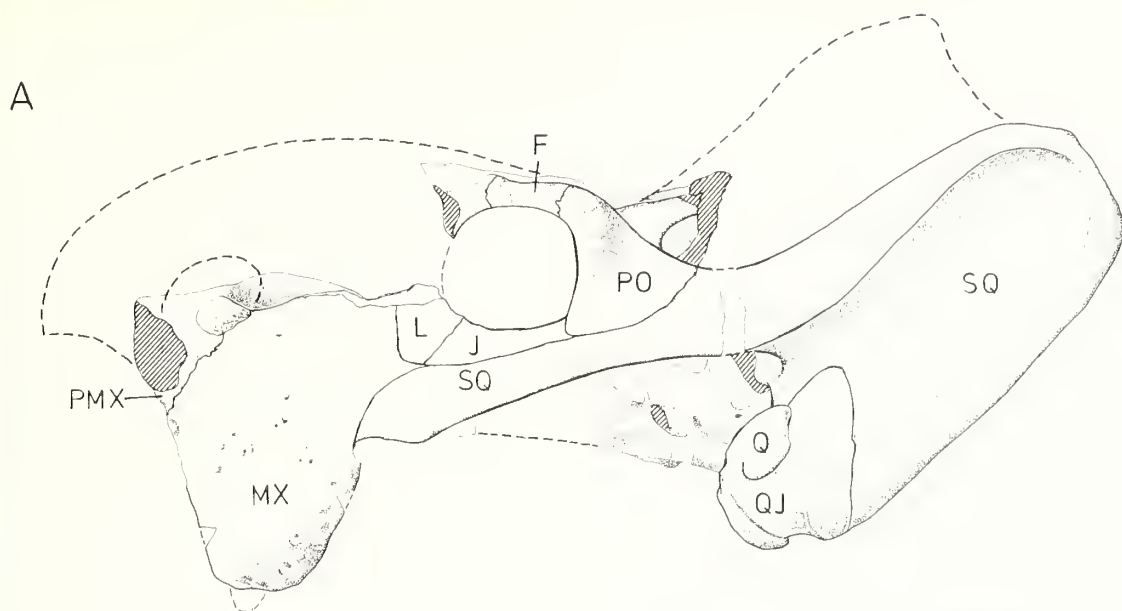
The dorso-medial region of the occiput is missing (Text-fig. 2B). The ventro-lateral corner of the squamosal extends a considerable distance lateral to the quadrate condyles. As is usually the case in large vertebrates, the foramen magnum is small in comparison with the size of the occipital condyle.

The nasal region of the snout has been crushed ventrally, and is not shown in lateral view (Text-fig. 3A). The suspensorium extends at a great angle antero-ventrally and runs smoothly into the zygomatic arch. The lower end of the post-orbital bar therefore lies not far antero-dorsally from the quadrate condyle. There is a deep pit between the main body of the quadrate and the quadratojugal, above the lateral quadrate condyle, which may have been the attachment area for a ligament restricting the anterior movement of the lower jaw. The outer surface of the posterior end of the zygomatic arch is concave dorso-ventrally. The ventral edge of the zygomatic arch below the orbit is quite sharp. The squamosal extends anteriorly to overlie the outer surface of the maxilla as far forwards as the posterior edge of the base of the caniniform process.

The secondary palate (Text-fig. 3B, C) is long and narrow, with almost vertical side walls. It is very deep, its surface lying 125 mm above the ventral end of the caniniform processes. The moderately-sized tusk emerges from the inner surface of the caniniform process, not from its apex. A rugose area extends dorsally from the root of the tusk on the inner side of the maxilla. The posterior edge of the caniniform process extends postero-laterally as a massive, rugose flange. Further posteriorly, a large foramen between the jugal, the maxilla, and the pterygoid runs dorsally into the maxillary antrum surrounding the base of the tusk. The mid-region of the palate, posterior to this point and anterior to the region around the interpterygoid vacuity, is missing.

The quadrate condyles (Text-fig. 3E) are orientated in an antero-medial direction; this area is not distorted, and this feature raises questions as to how the lower jaw functioned, since it is normally presumed to have had a simple antero-posterior sliding/rotating movement (e.g. Crompton and Hotton 1967). The interpterygoid vacuity (or fenestra medio-palatinalis, see Cox 1968, p. 13) and basicranial axis are well-preserved. The whole basicranial axis is greatly shortened. There is therefore only a very short median contact of the pterygoids behind the fenestra; this region is raised into a transverse, ventrally-projecting ridge, which lies only just anterior to the basisphenoid tubera. The internal carotid foramina can be seen piercing the parasphenoid. A

TEXT-FIG. 3. *Rechmisaurus cristarhynchus*; BM(NH) R11955, $\times 0.2$. A, lateral view. B, anterior view of snout. C, palatal view of snout. D, ventral view of basis cranii and quadrate region. E, lateral view of braincase. Abbreviations: BO, basioccipital; BSP, basisphenoid; F, frontal; IP, interparietal; J, jugal; L, lacrimal; MX, maxilla; PAL, palatine; PF, prefrontal; PMX, premaxilla; PO, postorbital; PSP, parasphenoid; PT, pterygoid; Q, quadrate; QJ, quadrato-jugal; SQ, squamosal; fen.ov., fenestra ovalis; i.c., internal carotid foramina; pr.cu., processus cultriformis of parasphenoid; sel.tu., sella turcica; Vid., Vidian canal; VII, foramen for facial nerve.



little antero-dorsal to these, a pair of foramina on either side are the openings for the anterior branch of the internal carotid artery and for the palatal branch of the VIIth cranial nerve; they open from within a short recess, which is therefore a truncated Vidian canal (Text-fig. 3E, F, i.c.). The foramen through which the main trunk of the VIIth cranial nerve exits from the braincase can be seen anterior to the fenestra ovalis (Text-fig. 3F, VII).

THE TAXONOMIC POSITION OF THE MANDA SPECIMEN

Though the skull is incomplete, it shows a number of features that suggest its taxonomic identity. The acute angle between the intertemporal bar and the interorbital region, the moderately elongated snout with a median nasal ridge, and the antero-ventrally directed suspensorium, are all diagnostic features of the kannemeyeriid dicynodonts, as slightly differently defined by Cox and Li (1983) and King (1988). Comparisons between the Manda specimen and other kannemeyeriids show that the most obvious similarities are with *Shaanbeikannemeyeria* Cheng, 1980, from the Er-Ma-Ying Formation of China. Both have wedge-shaped skulls, strong rugose maxillae, a narrow intertemporal bar that nevertheless has a slight median longitudinal groove, and a very short interpterygoid vacuity and median pterygoid neck between that vacuity and the parasphenoid. However, further comparison shows that all these features are present also in *Rechnisaurus* (Chowdhury 1970; Bandyopadhyay 1989) from the Yerrapalli Formation of India, and detailed comparison of the drawings and descriptions of Cheng and Chowdhury leave no doubt that the two genera are identical. Cheng did not compare his Chinese dicynodont with Chowdhury's 1970 genus, but that was possibly because Keyser and Cruickshank (1979) had erroneously concluded that *Rechnisaurus* was a junior synonym of *Kannemeyeria* (Bandyopadhyay 1989).

The Chinese species must therefore be known as *Rechnisaurus xilougouensis* (Cheng), and it can be distinguished from the Indian species, *R. cristarhynchus*, by the fact that the premaxillae and frontals project medially into the frontals. A third species, *Shaanbeikannemeyeria buerdongia* from the lower Er-Ma-Ying Formation of Inner Mongolia, was described by Li (1980), and must now be renamed *Rechnisaurus buerdongia* (Li); it differs from the other species in having smaller maxillary processes.

The incompleteness of the African specimen makes it difficult to compare with the other species. However, it is identical to the Indian specimen in the unusual feature that the squamosal extends far forwards to reach the base of the caniniform process of the maxilla. The only differences between the two specimens are that the canine tusk is smaller than in the Indian specimen and that it has a strong ridge around the posterior rim of the interpterygoid vacuity, while the Indian species shows no ridge. The Manda specimen is accordingly regarded only as an additional specimen of *Rechnisaurus cristarhynchus* Chowdhury. Accordingly, the missing postero-dorsal part of the skull and the dorsal outline of the snout in Text-figures 2A, B and 3A have been restored as in *R. cristarhynchus*.

When it was collected, two features of the Manda specimen recalled advanced kannemeyeriids such as *Placerias*: its short interpterygoid vacuity, and the fact that its tusk emerges from the inner side of the caniniform process rather than from its apex. This is probably the basis for Keyser's (1980, p. 62) statement that 'A species that resembles *Ischigualastia* from the Santa Maria and Ischigualasto Formations of South America has been found in the Manda Beds of Tanzania.' (In fact, *Ischigualastia* is not known from the Santa Maria Formation.)

Another dicynodont from the Manda Formation, *Sangusaurus* (Cox 1969) has been described by Cruickshank (1986). It shares many features with the holotype of *R. cristarhynchus*, including a small boss just posterior to the pineal foramen, a feature otherwise unknown in Triassic dicynodonts. It is possible that these two genera are congeneric, despite the fact that *Sangusaurus* is tuskless and has a more pointed premaxilla (Table 1).

Rechnisaurus was thus widely distributed in Pangaea, being found in two localities in Gondwana, and two localities in Asia, some 16,000 km away around the western end of the Tethys Sea. Both these areas lie in the Triassic temperate regions and, as Parrish, Parrish, and Ziegler (1986) point out, no Lower or Middle Triassic therapsids have been found between palaeolatitudes 35° N and

35° S, in the tropical regions. The absence of *Rechnisaurus* from this intermediate belt of latitudes is thus merely part of a more general pattern. The presence of species of that genus both north and south of this tropical band shows that this therapsid, at least, was able to traverse this area. The absence of fossils therefore suggests that conditions there were unsuitable for fossilization, rather than that therapsids did not inhabit these regions. A similar pattern of absence of Triassic tetrapod fossils in general from an equatorial band of latitudes has already been documented (Cox 1973a).

TABLE 1. Cranial features of kannemeyeriid dicynodonts.

	IT/IO at angle	Quadrate forwards	Strong maxilla	Tusks	Midnasal ridge	Blunt snout	Wedge- shaped skull
<i>Kannemeyeria</i>	+	—	+	+	+	+	+
<i>Rechnisaurus</i>	+	+	+	+	+	+	+
<i>Uralokannemeyeria</i>	+	+	+	+	+	+	+
<i>Rabidosaurus</i>	+	+	?	+	+	—	?
<i>Sangusaurus</i>	+	+	+	+	+	?	+
<i>Wadisasaurus</i>	+	+	±	±	+	+	—
<i>Ischigualastia</i>	+	+	—	—	—	—	+
<i>Jachaleria</i>	+	+	—	—	—	—	+
<i>Placerias</i>	+	+	+	+	—	—	+
* <i>Moghreberia</i>	+	+	+	+	?	—	+

+ = character present; — = character absent; ± = character present in some specimens, absent in others; ? = character unknown; * = see text; IT = intertemporal bar; IO = interorbital bar.

The relationships of Rechnisaurus. *Rechnisaurus* shows a number of features that appear to a greater or lesser extent in several other Triassic dicynodonts (Table 1): pronounced angulation between the intertemporal bar and the frontal region, pointed out by King (1988); an antero-ventrally directed suspensorium; a strong maxilla, usually bearing a tusk and with a rugose antero-ventral flange; a median nasal ridge; a skull that is wedge-shaped in dorsal view, and a bluntly pointed snout. The Family Kannemeyeriidae of Cox and Li (1983) begins with the Early Triassic *Kannemeyeria*, in which the suspensorium is directed ventrally. It continues with a number of Middle Triassic genera (*Rechnisaurus*, *Uralokannemeyeria*, *Rabidosaurus*, *Sangusaurus*, *Wadisasaurus*), in which the suspensorium is directed more antero-ventrally. In all these genera the snout is bluntly pointed and bears a median dorsal nasal ridge. In *Wadisasaurus* and in the Late Triassic genera (*Ischigualastia*, *Jachaleria*, *Placerias*, * *Moghreberia*), the snout has become pointed and lacks this ridge. In the tuskless members of the group (*Jachaleria*, *Ischigualastia*) the maxilla is, not surprisingly, less well-developed than in the remaining genera—a correlation between these two features is strongly supported by the fact that, in *Wadisasaurus*, some specimens (presumably male) are tusked and have a strong maxilla, while others (presumably female) are tuskless and have a poorly developed maxilla (Bandyopadhyay 1988). (The poorly preserved skull of *Moghreberia* Dutuit, 1980 seems so similar to that of *Placerias* Camp and Welles, 1956 that these two genera may well prove to be identical, while the few fragments of *Azarifeneria* Dutuit, 1989 are very similar to the corresponding portions of *Ischigualastia* Cox 1965.)

King has recently (1988) provided a new classification of Triassic dicynodonts, which differs in several respects from that of Cox and Li (1983). As she rightly comments (King 1988, p. 69), 'Until a complete revision of the Middle and Late Triassic material, using first-hand information, is undertaken, no absolute consensus of opinion on their relationships can be expected.' A difference between the two classifications is that King separates *Ischigualastia* and *Placerias* from the kannemeyeriids, and links them more closely with the *Zambiasaurus-Stahleckeria* group. This is

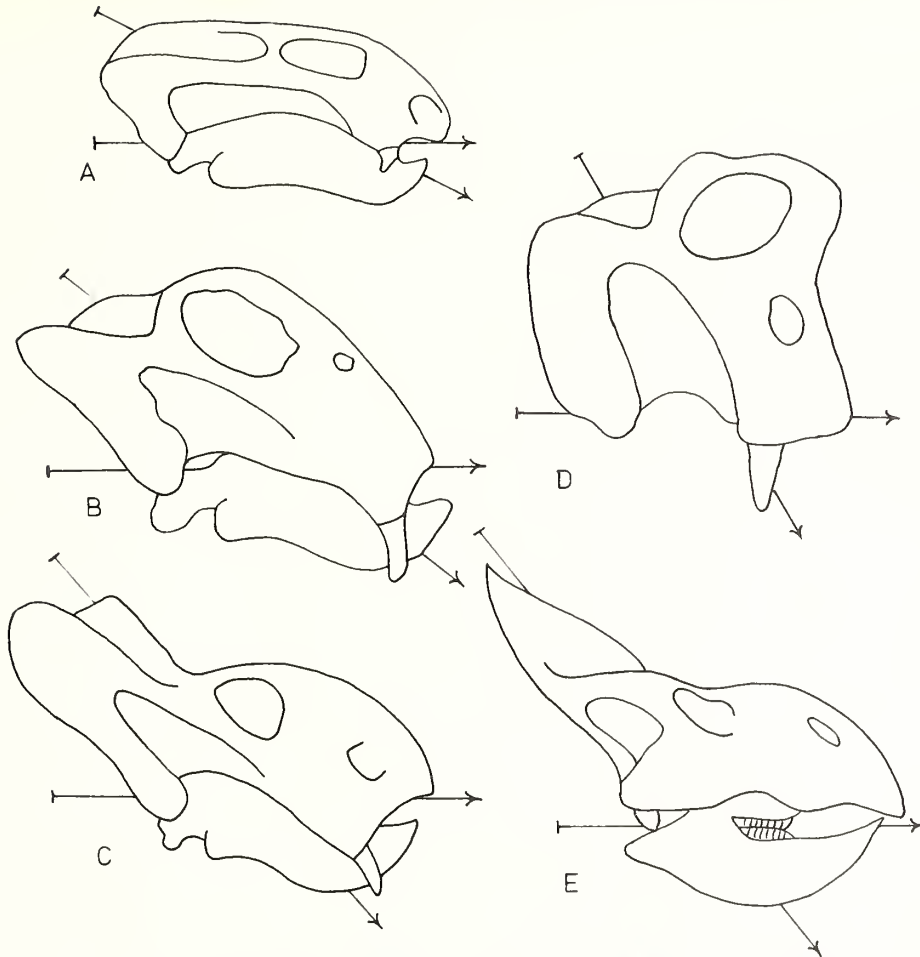
despite the great difference between the shapes of the occipital plates and snouts of these two groups (Cox 1965), and despite the fact that it is then necessary to suggest that a long, high intertemporal bar at an angle to the frontal region evolved independently in the *Kannemeyeria* group and in the *Placerias* group.

The feature that unites the *Placerias* group to the *Stahleckeria* group (and also to the *Sinokannemeyeria* group) in King's (1988) cladogram is that the parietals are covered incompletely by the postorbitals. She here refers to a condition in which the postorbital did not extend as far posteriorly as the parietal-interparietal suture, so that the posterior parts of the parietals are exposed in the skull roof. King (1990, p. 225) defines the character as merely 'Postorbitals do not extend far posteriorly'. This is indeed true of *Ischigualastia* and *Placerias*. But in *Stahleckeria* the posterior extent of the postorbital is uncertain: Huene reconstructs it as extending posteriorly to meet the squamosal in his skull no. 2 (Huene 1935, pl. 5), but Camp's (1956, fig. 45) drawings of a cast of the same specimen show a short postorbital. In her diagnosis of the genus *Stahleckeria* King (1988, pp. 107–108), makes no statement on this character. In the other stahleckeriid genus, *Zambiasaurus*, the postorbital appears to have extended back as far as the junction between the parietal and the interparietal (Cox 1969). The posterior parts of the parietal are indeed exposed in all of these genera, but this would be true irrespective of the posterior extent of the postorbital, because the latter bone is lateral to the wide parietal, rather than dorsal to it.

According to King (1988, 1990), the features of the postorbital and parietal mentioned above are found in the *Sinokannemeyeria* group (which includes also *Parakannemeyeria*, *Uralokannemeyeria*, *Dinodontosaurus*, and *Rhadiodromus*), as well as in the *Placerias* and *Stahleckeria* groups. However, though the postorbital does not extend far posteriorly in *Dinodontosaurus*, it does so in *Sinokannemeyeria* and *Parakannemeyeria* (Sun 1963) and *Uralokannemeyeria* (Danilov 1971); the situation in *Rhadiodromus* (Kalandadze 1970) is uncertain. The posterior part of the parietal is widely exposed in all these genera except *Parakannemeyeria*, but this 'genus' may merely consist of skulls of *Sinokannemeyeria* that have been compressed laterally, those of the latter genus having instead been compressed dorso-ventrally. *Sinokannemeyeria* has a wide snout, with canine teeth set wide apart and projecting backwards, a wide intertemporal bar between the postorbitals, and a low, wide occiput. *Parakannemeyeria* has a narrow snout, with canine teeth set close together, a narrow intertemporal bar covered by the postorbital bones, and a high, narrow occiput. These are exactly the differences that might be expected if the two sets of skulls had been affected by the two different types of plastic deformation that would have resulted from the different orientations of deposition. The two genera are both from the Er-Ma-Ying Formation of China (Sun 1963, 1989b).

The exposure of the parietal, which King does not mention in her (1990) list of taxonomic characters, thus appears in this case to be more reliable than the degree of posterior elongation of the postorbitals, which she retains as a character. But such an osteological detail has no obvious adaptive value in itself, and may arise from quite different skull shapes. For example, the parietal is likely to be exposed if the intertemporal bar is extended postero-dorsally into a crest, far away from the centres of ossification of the postorbitals. But it is also likely to be exposed if the intertemporal bar is very wide, as in *Lystrosaurus*. It is therefore preferable to try to identify the underlying adaptive changes that may in turn have led to the appearance of these features. In the case of the postero-dorsal extension of the intertemporal bar, one of the features that unites the *Placerias* group with the kannemeyeriid group, this change seems to involve a fundamental change in the jaw muscle system, to meet an adaptive need that *Lystrosaurus* achieved in a different way, as follows.

Most Permian dicynodont genera have a long, low skull, in which the intertemporal-interorbital bar, like the zygomatic arch and the palatal surface, are parallel with one another. The posterior edge of the maxilla and the suspensorium leading down to the palate are also parallel to one another, but run antero-ventrally. In the Permian dicynodont *Emydops* (Crompton and Hotton 1967), the adductor muscles run at a shallow angle (*c.* 35°) down to the lower jaw because of the long, low skull. The horizontal component of their action is therefore much stronger than the vertical component, and there is little vertical bite force (Text-fig. 4A). Extra attachment surface for



TEXT-FIG. 4. Lateral views of skulls of A, *Emydops*; B, *Lystrosaurus ?murrayi*; C, *Reclinisaurus cristarhynchus*; D, *Lystrosaurus mccaigi*; E, *Protoceratops*. Axes indicate direction of action of adductor internus jaw muscles from postero-lateral corner of temporal vacuity, and jaw axis from quadrate condyle along surface of palate. The distances between the anterior surfaces of the quadrate condyles and the anterior end of the snout are the same in drawings A-C and E. (A and B, after Crompton and Hotton 1967; C, skull after Cheng 1980, lower jaw from *Kannemeyeria* after Camp 1956; D, after Brink 1952; E, after Dodson 1976.)

the inner portion of the adductor muscles is provided by the postorbital bones extending as wings projecting laterally from the intertemporal bar.

In *Lystrosaurus* (Text-fig. 4B), a greater vertical component to the action of the adductor muscles has been achieved by shortening the skull, as noted by Cluver (1971). In order not to reduce the length of these muscles, which would have reduced the gape, the whole palatal structure has been moved antero-ventrally, paralleled by a similar antero-ventral extension of the suspensorium. The whole muscle mass is now at a steeper angle to the palatal surface (*c.* 50°), and is therefore accommodated in a more vertically-orientated column, and the temporal vacuity is shorter. Because the palate has extended anteriorly, the snout in contrast is longer as well as deeper. Postorbital wings still project laterally from the intertemporal bar.

The resulting skull morphology, in which the orbit and nostril remain dorsally placed, has been likened to that of a hippopotamus, and it has therefore been suggested that *Lystrosaurus* was semi-

aquatic (Broom 1902; Watson 1912). Though, in the specimen described by Crompton and Hopson (1967), which appears from their illustrations to be a specimen of *Lystrosaurus murrayi*, the external nostril is at the level of the ventral edge of the orbit, that of *Lystrosaurus mccaigi* is placed below the orbit (Text-fig. 4D). Brink (1951) states that there was a groove running dorsally from the postero-dorsal margin of the external naris in this species, and suggests that fleshy nostrils were directed upwards to open in front of the eyes, but the morphology is certainly not clearly indicative of semi-aquatic life. The jaw muscles in *L. mccaigi* would have been the most dorso-ventrally directed (c. 60°) of those of any dicynodont. They would therefore have been the most powerful and, as Watson (1912) comments in the context of the massiveness of the jaws of *Lystrosaurus*, this is difficult to reconcile with the softness of most aquatic plants. Watson also notes that the powerful sacrum of *Lystrosaurus* is surprising in an aquatic animal (though it would not be as surprising in a semi-aquatic animal that had to support its weight on land for long periods). Earlier, Broom (1903) had stated that the shoulder-girdle of *Lystrosaurus* was different from that of other dicynodonts in having a smaller interclavicle and a larger sternum. He suggested that this was somehow correlated with an aquatic life, but did not explain this.

Nothing indicates that the earlier or later dicynodonts were semi-aquatic, so *Lystrosaurus* would represent a brief, unique aquatic excursion. It would also be surprising to find this unusual environment suddenly very widespread in the world at the time of *Lystrosaurus*, for the genus is known from deposits in Africa, Antarctica, India, European Russia, and China. King (pers. comm. 1989; 1991) has come to the same conclusion, that *Lystrosaurus* was not aquatic, independently. None of the arguments is conclusive, but they suggest that the matter requires re-evaluation.

Kannemeyeriids appear to have achieved an orientation of the adductor muscles similar to that of the lystrosaurids, but partly by an antero-ventral movement of the palate and partly by a postero-dorsal extension of the intertemporal bar (Text-fig. 4C). The adductor muscle mass now runs at an angle of c. 50° to the palate, and almost parallel to the intertemporal bar. As a result, the lateral postorbital wings to the intertemporal bar are lost, because they are no longer at an appropriate angle to provide attachment for the adductor muscles, and would have obstructed the access of these muscles to the more postero-dorsal part of the intertemporal bar.

Chrulaw (1976) noted the general similarity between the skull architecture of dicynodonts and that of ceratopsian dinosaurs, comparing only *Dicynodon* and *Lystrosaurus* with *Triceratops*, in which the parieto-squamosal 'frill' extends more posteriorly than horizontally. The skull architecture of kannemeyeriids is instead similar to that of the primitive ceratopsian dinosaur *Protoceratops* (Text-fig. 4E). In that genus, as in the kannemeyeriids, the skull is postero-dorsally extended to provide a greater length for the jaw muscles (Haas 1955; Ostrom 1966) which run at about 50° to the axis of the lower jaw, and there is a narrow, horny beak on the anterior end of both the upper and lower jaws. In the ceratopsians, however, there is a battery of cutting teeth posterior to the beak, and later ceratopsians developed a coronoid process and a greatly elongated posterior 'frill' to the skull to improve the mechanics of the use of this posterior dentition. Ostrom (1966) suggests that this system, in which only antero-posterior jaw movements were possible, was particularly adapted for chopping up fibrous food, and that the Late Cretaceous ceratopsians may have fed on the leaves of cycads and palms.

The kannemeyeriids thus appear to have an advanced feeding system, and it may be no coincidence that they survived (as the Late Carnian *Placerias* group) longer than any other dicynodont. These Late Triassic kannemeyeriids are also the only dicynodonts found in the Triassic tropics (cf. Parrish, Parrish and Ziegler 1986), and had a much more extremely pointed premaxilla than their earlier Triassic kannemeyeriid relatives. The stahleckeriids, by contrast, appear to have increased the area available for insertion of the jaw muscles mainly by lateral expansion of the squamosals, and had a very blunt anterior end to the premaxilla; it may also be no coincidence that this group became extinct during the Middle Triassic, perhaps because of competition from advanced rhynchosaurs and gomphodonts, or because of a diminution in their preferred plant food.

RELATIVE AGES OF THE TRIASSIC DICYNODONT-BEARING FAUNAS

Triassic dicynodonts, being large and common terrestrial herbivores, are useful in documenting Triassic biogeography and stratigraphy. Anderson and Anderson's (1970) review of Triassic stratigraphy was mainly a statement of opinion, it lacked systematic discussion of the data upon which it was based, and was confined to Gondwana biostratigraphy. Their views, as reflected in a later paper on Permo-Triassic tetrapod distribution (Anderson and Cruickshank 1978) have been followed in King's (1988) review of the Dicynodontia. The following review integrates work since 1970 on new faunas, reassigned genera, and redated faunas and their implications for dicynodont evolution and taxonomy.

The earliest Triassic dicynodont is *Lystrosaurus* from the *Lystrosaurus* Zone of South Africa, and the Fremouw Formation of Antarctica, the Panchet Formation of India, the Ryabinian horizon of European Russia, and the Chiu-T'sai-Yuan-Tze Formation of China (Colbert 1982). (An isolated dicynodont quadrate bone from Australia was identified as that of *Lystrosaurus* by Thulborn (1983) but, as pointed out by King (1983), it is impossible to identify it to generic level.)

The *Lystrosaurus* fauna contains rhytidosteid amphibians, found in several parts of the world, but only in formations of early Scythian (Griesbachian-Smithian) age (Cosgriff 1984). The most direct evidence of the age of these faunas is the rhytidosteid *Deltasaurus* in the marine Kockatea Shales of Western Australia, a close relative of *Rhytidosteus* of the *Cynognathus* Zone of South Africa. The Kockatea Shale contains ammonites and a microflora suggesting a Lower Scythian age – either Smithian (Anderson and Cruickshank 1978; Camp and Banks 1978) or, according to Banks (1978), Dienerian. Lozovskiy (1985) has also independently dated the *Lystrosaurus* beds of the Moscow basin as lowest Triassic, based on fresh-water conchostracans.

Above the *Lystrosaurus* Zone in South Africa lies the *Cynognathus* Zone, but it has long been recognized (Cosgriff 1984) that there is a sharp break between these two. The characteristic dicynodont is *Kannemeyeria*. An association between *Kannemeyeria* and other large dicynodonts has been reported from two faunas, but both these reports have since been shown to be erroneous. Crozier (1970) identified two dicynodonts from the lower fossiliferous horizon of the N'tawere Formation of Zambia, recognizing one as a new species of *Kannemeyeria*, and the other as *Rechnisaurus cristarhynchus*. However, Keyser and Cruickshank (1979) and Bandyopadhyay (1989) have shown that the latter specimen is quite different from *Rechnisaurus*, and appears to belong to *Kannemeyeria*, which is thus the only dicynodont from this horizon in the N'tawere Formation. The presence of the cynodont *Diademodon* in this horizon as well as in the *Cynognathus* Zone of South Africa further supports the view that these two formations are of similar age (Cox 1969).

Kannemeyeria was also described by Cruickshank (1965) from the Manda Formation of Tanzania, in which *Rechnisaurus* is also found, but he has since shown (1986) that the specimen instead came from the underlying Kingori Sandstone Formation.

Both *Kannemeyeria* and *Diademodon* are found in the Omingonde Formation of South West Africa (Keyser 1973), which therefore also appears to be of an age similar to that of the *Cynognathus* Zone. However, the presence of *Titanogomphodon*, which is more advanced than the other diademodonts in having a secondary basin on the crowns of the molariform teeth (Keyser 1973), suggests that the Formation may be of slightly later date.

Kannemeyeria is thus known from the *Cynognathus* Zone of South Africa and from deposits in other parts of Africa (Zambia, Tanzania, South-West Africa), that are therefore presumably of similar age. It is also known from the upper part of the Puesto Viejo Formation of Argentina (Bonaparte 1966), accompanied by the cynodont *Cynognathus* – the zone fossil of the *Cynognathus* Zone. *Kannemeyeria* is therefore known only from south-western Gondwana.

The *Cynognathus* Zone is commonly viewed as being of late Early Triassic age (e.g. Anderson and Anderson 1970), but there is no way in which its age can be determined in terms of the classic European non-marine German sequence or marine Alpine sequence. All that can be attempted for the succeeding Triassic faunas is to place them in relative order – and even this is complicated by ecological biases of some of the faunas, and by recent re-assignments of some synapsid genera.

The next-youngest diverse, well-documented Triassic fauna is that of the Manda Formation of Tanzania. This contains traversodontid cynodonts and rauisuchid thecodonts, which are absent from the *Cynognathus* Zone. It also contains the rhynchosaur *Stenaulorhynchus*, while the only rhynchosaurs in the *Cynognathus* Zone are *Howesia* and *Mesosuchus*, which are more primitive in lacking the interlocking blade and groove jaw apparatus of the later rhynchosaurs (Benton 1980, 1983). There is therefore little doubt that the Manda Formation is of later age than the *Cynognathus* Zone. Its exact age cannot be directly established, but the Manda rhynchosaur *Stenaulorhynchus* is closest to *Rhynchosaurus* (Benton 1983), which is found in England both in the Midlands and in the Otter Sandstone Formation of Devon (Benton 1990). The age of the Midlands species is difficult to establish, different elements in the faunal and floral assemblage being interpreted to indicate ages ranging from Late Scythian to Late Ladinian (Benton 1990). However, the age of the Otter Sandstone vertebrate fauna, which includes fishes, amphibians and reptiles, may be Anisian (Milner *et al.* 1990).

Manda dicynodont genera are found also in three other faunas, *Rechnisaurus* in the Yerrapalli Formation of India and in the Er-Ma-Ying Formation of China, and *Sangusaurus* in the upper fossiliferous horizon of the N'tawere Formation of Zambia (Cruickshank 1986). The Yerrapalli fauna contains the dicynodonts *Rechnisaurus* and *Wadisasaurus*, an erythrosuchid and a prestosuchid thecodontian, a trirachodont cynodont, and a labyrinthodont amphibian (Bandyopadhyay 1988). The age of the Er-Ma-Ying Formation is somewhat perplexing. It is now divided into upper and lower portions (Sun 1989). The faunas of each portion contain thecodontian reptiles similar to genera in the *Cynognathus* Zone of South Africa: *Halazhaisuchus* of the lower portion and *Shansisuchus* of the upper portion are respectively similar to *Euparkeria* and to *Erythrosuchus* of the *Cynognathus* Zone (Sun 1989). This seems to suggest that both faunas are similar in age to the South African fauna, but the lower fauna also contains *Rechnisaurus* (*Shaanbeikannemeyeria*), which is found also in the Manda fauna. *Rechnisaurus* in the Er-Ma-Ying Formation suggests an age similar to the Manda Formation, while the other elements must be seen as anomalous, perhaps due to the considerable distance between the Chinese and African faunas. The upper fossiliferous horizon of the N'tawere Formation of Zambia contains the dicynodonts *Sangusaurus* (Cruickshank 1986) and *Zambiasaurus*, the traversodont cynodont *Luangwa*, and fragments of thecodontians.

Manda-like dicynodonts in the Donguz Formation of European Russia include *Rabidosaurus*, *Rhadiodromus* (= *Rhinocerocephalus*), and *Rhinodicynodon* (Kalandadze 1970), and *Uralokannemeyeria* (Danilov 1971). Apart from the shansiodont *Rhinodicynodon*, all of these are very similar to *Rechnisaurus* in skull proportions. Three other dicynodont genera from the Donguz Formation have been described more recently, but these (*Edaxosaurus*, *Elatosaurus*, and *Calleonasus*; Kalandadze and Sennikov 1986) are known only from respectively an 'upper jaw bone' and two nasal bones, and are effectively *nomina nuda*. The rest of the Donguz fauna comprises temnospondyl amphibians (the capitosaur *Eryosuchus*, Ochev 1966; plagiosaurs, Shishkin 1986), the procolophonid *Orenburgia* (Ochev 1968; Ivakhnenko 1977); thecodontians (*Dongusia*, 'Erythrosuchus' Ochev 1980; *Vyushkovisaurus* Ochev 1982; *Vytshegdosuchus*, *Dongosuchus* Sennikov 1988), and traversodont cynodonts (Tatarinov 1974, 1988). The thecodontians are fragmentary, and the other groups are from such long-lived lineages that they provide little information on the age of the Donguz Formation. Thus, unfortunately, one can only rely on the slender evidence of the similarities of the *Rechnisaurus*-like dicynodonts discussed above, and provisionally view it as if similar age.

As noted earlier, the Manda Formation cannot be dated more precisely than Anisian. The other four faunas just discussed offer such poor evidence on dating that they are all ascribed provisionally to the Anisian, this reflecting also the fact that they appear to be later than the Scythian *Cynognathus* Zone fauna, and earlier than the South American faunas to be discussed next.

The South American dicynodont faunas include those of the Chañares and Ischigualasto Formations of Argentina, and of the Santa Maria Formation of Brazil. Cox (1965, 1968, 1973b), and Bonaparte (1982) have discussed the relative ages of these South American Middle-Late Triassic faunas. An important new element has been the documentation by Barberena (1977) of the

consistent differences between two faunal assemblages in the Santa Maria Formation, which now makes it possible to resolve some apparent anomalies. The fact that the Santa Maria fauna included the rhynchosaur *Scaphonyx* (also known from the Ischigualasto fauna) and the early dinosaur *Staurikosaurus* gave the impression that the whole Santa Maria fauna must be considerably younger than the Manda fauna (Cox 1965, 1968, 1973). However, Barberena (1977) has since shown that these elements are found only in deposits near the town of Santa Maria. He names this the Rhynchocephalian Assemblage, but now that it has been realized that rhynchosaurs and sphenodontids are not closely related (Carroll 1977), a more appropriate name would be the Rhynchosaur Assemblage; its age is discussed below.

Barberena (1977) points out that the rhynchosaurs, abundant in this Rhynchosaur Assemblage, are wholly lacking in deposits from the Xiniquá and Pinheiros areas, respectively to the west and to the east of Santa Maria; these localities instead contain an abundance of stahleckerioid dicynodonts (*Stahleckeria* and *Dinodontosaurus*), as well as chiniquodont cynodonts. He names this fauna the Therapsid Assemblage. (Though he shows the kannemeyerioid dicynodont *Jachaleria* as found in this Assemblage, Bonaparte (1982) states that it is instead from the much later Caturritá Formation of Brazil.)

Dinodontosaurus and the traversodont cynodont *Massetognathus* (Hopson and Kitching 1972) are found also in the Chañares Formation of Argentina. In addition to these similarities at generic level, the two faunas are similar in containing chiniquodont cynodonts and in lacking rhynchosaurs. They therefore appear to be of very similar, if not identical, age and character. It is difficult to estimate that age precisely, since the chiniquodont cynodonts range widely in age, from the Early Triassic Manda fauna to the Late Triassic Argentinian faunas of Ischigualasto and Las Esquina (Hopson and Kitching 1972; Bonaparte 1982). However, the Chañares herbivorous cynodonts do appear to be somewhat more advanced than those of the Manda fauna (Romer 1967). This suggests that the Chañares/Santa Maria Therapsid Assemblage is later in age than the Manda fauna, and may therefore be provisionally placed in the Ladinian.

Barberena (1977) rightly points out that the discovery that the Rhynchosaur Assemblage is younger than the Therapsid Assemblage makes it unnecessary to postulate that merely ecological differences were the reason why rhynchosaurs and dicynodonts had not been found together. However, since rhynchosaurs were present in the Manda fauna, which is clearly older than the Therapsid Assemblage, a problem remains. The absence of rhynchosaurs from the Chañares/Santa Maria Therapsid fauna must have been caused by either geographical or ecological factors.

A geographical cause, in the sense of a geographical barrier between the South American and East African localities, seems unlikely. Apart from the general similarities in Triassic faunas throughout Pangaea (Cox 1973a), the dicynodont *Kannemeyeria* is found in both Africa and Argentina, the Brazilian dicynodont *Stahleckeria* is closely related to the Zambian genus *Zambiasaurus* (Cox 1969), and the rhynchosaur *Steuatorhynchus* of the Manda Formation is related to *Rhynchosaurus* of Britain (Benton 1983).

An ecological explanation therefore remains more plausible, though its precise nature can only be guessed at. Rhynchosaurs were clearly herbivorous (Benton 1983), and therefore may well have competed with dicynodonts. Though the two groups co-exist in the Manda fauna, it may be that the climatic conditions of the South American areas, far closer to the periphery of a Gondwana continent that still lacked Andean mountains, may have been moister and may have encouraged a lush flora, which may have favoured the dicynodonts. The two groups again co-exist in the Late Triassic Ischigualasto fauna, but the stahleckerioid dicynodonts of the Chañares/Santa Maria Therapsid Assemblage had by then disappeared, and only the kannemeyeriids co-existed with the rhynchosaurs.

The next-youngest dicynodont-bearing faunas are those of the Ischigualasto Formation of Argentina, the Chinle Formation of North America, and the Argana Formation of Morocco. Only the kannemeyerioid type of dicynodont is found in these. Their ages have recently been re-evaluated by Olson and Sues (1986), on the basis of palynoflorule and plant megafossil evidence, and they are now considered to be of Late Carnian age (though this evidence is indirect, rather than direct

interfingering of terrestrial and marine deposits). The presence of the phytosaur *Paleorhinus* in the Moroccan fauna as well as in the Dockum Formation of Texas and in the Popo Agie Member of the Chugwater Formation of Wyoming also suggests an age no later than the Late Carnian (Ballew 1989), and Litwin (1986) similarly suggests a Late Carnian age for the Lower Unit of the Petrified Forest Member of the Chinle Formation (which contains *Placerias*) on the basis of its plant spores. Hunt and Lucas have also very recently (1991) suggested a Late Carnian age for these faunas on the basis of the presence in all of them of elements coeval with the phytosaur *Paleorhinus* of the German Blasensandstein.

If such a Late Carnian age is provisionally accepted for the Ischigualasto fauna, the question arises as to what age should be assigned for the Santa Maria Rhynchosaur Assemblage. The presence of the rhynchosaur *Scaphonyx* in both faunas suggests that there is no great difference in their ages. This is supported by Hopson's (1985) restudy of the traversodont cynodont *Gomphodontosuchus braziliensis* from the Rhynchosaur Assemblage, which shows that it is probably a juvenile specimen closely related to *Exaeretodon* of the Ischigualasto fauna. The Rhynchosaur Assemblage, also, is therefore given a Late Carnian age in Table 2.

However, the Ischigualasto fauna differs from the Chinle/Dockum fauna, as it is still dominated by mammal-like reptiles such as the dicynodonts and cynodonts, while the North American faunas are instead dominated by archosaurs such as the thecodontians and early dinosaurs. Though there may also be an ecological component to these differences, they suggest that the Ischigualasto fauna is rather more archaic and older than the North American faunas.

The last known dicynodont is *Jachaleria* from the Los Colorados Formation of Argentina (Bonaparte 1971) and from the Caturritá Formation of Brazil (Araújo and Gonzaga 1980). This genus is clearly very closely related to *Ischigualastia* (Table 1: Araújo and Gonzaga [1980] state that the posterior orientation of the suspensorium in *Jachaleria* and the curved shape of the zygomatic arches in *Ischigualastia* are probably the result of distortion), which suggests that these formations are not very much later in time than those mentioned in the preceding paragraph, and they too are given a Late Carnian date.

TABLE 2. Relative ages of Triassic dicynodont-bearing strata (figures indicate age in millions of years, from Cowie and Bassett 1989).

220	Late Carnian	Los Colorados; Caturritá; Chinle
	Late Carnian	Ischigualasto; Argana; Santa Maria Rhynchosaur Assemblage
230	Ladinian	Santa Maria Therapsid Assemblage; Chañares
235	Anisian	Manda; Upper N'tawere; Yerrapalli; Donguz; Omingonde; Er-Ma-Ying
240	Late Scythian	<i>Cynognathus</i> Zone; Lower N'tawere; upper Puesto Viejo
	Early Scythian	<i>Lystrosaurus</i> Zone; Panchet; Ryabinian horizon; Chiu-T'sai-Yuan-Tze; Fremouw; lower Puesto Viejo
250		

The sequence of Triassic dicynodont-bearing faunas that results from the above review is shown in Table 2. It cannot be too strongly emphasized that the relative ages of these faunas are considered to be much more reliable than their absolute ages in terms of the Scythian–Carnian classic sequence.

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IMMUNOLOGICAL INVESTIGATIONS OF RELATIONSHIPS WITHIN THE TEREBRATULID BRACHIOPODS

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ABSTRACT. Intra-crystalline macromolecules isolated from the skeletons of nine species of Recent articulate brachiopods were compared by enzyme linked immunosorbent assay (ELISA) to assess the relationships within the Order Terebratulida (Phylum Brachiopoda, Class Articulata). Immunological distance data indicated that the sub-division of this order into three suborders (based on the characteristics of the internal skeleton, particularly the brachial loop) is not valid. Three major clusters were recognized within the Terebratulida which approximately correspond to recognized superfamilies, with the exception that the family Kraussinidae (possessing a long brachial loop) is placed within the Terebratulacea (characterized by a short loop). The three lineages are more closely related to each other than was previously predicted, and yet within most lineages there is a greater degree of subsequent diversification than has hitherto been recognized. The independent evolution of long brachial loops in two lineages identified by the immunological data, highlights problems with using the internal skeleton as a high-level taxonomic character within the terebratellids.

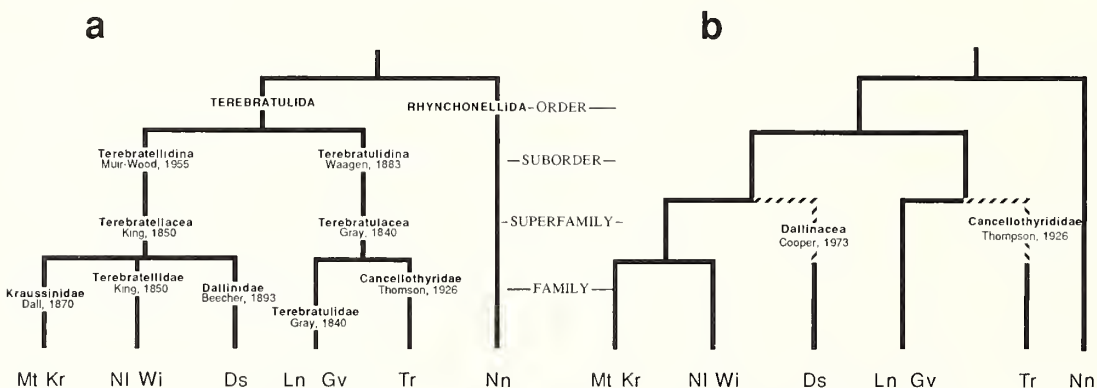
THE Terebratulida is the largest extant order of brachiopods, being characterized by the possession of an internal skeleton (brachidium or brachial loop) which in life supports the lophophore. A taxonomic treatment incorporating patterns of loop development was first elaborated by Beecher (1893), extended by Muir-Wood (1955), and utilized in the Treatise (Williams *et al.* 1965) in which the Order Terebratulida is divided into three suborders on the basis of the ontogeny and form of loop development. Two suborders characterized as possessing either short- (Terebratulidina) or long-loops (Terebratellidina), contain extant members; the third (Centronellida) is extinct. The prevailing taxonomic situation of the extant families is summarized by Collins *et al.* (1988); although inadequacies within the systematics of the Terebratulida have been recognized (e.g. Richardson 1975; Elliott 1976; Williams and Hurst 1977) the essential sub-division has remained unchallenged (Text-fig. 1a).

In the earlier immunological study, we presented data which appeared to challenge the primacy of loop length as a subordinal character within the terebratulids (Collins *et al.* 1988). No immunological distances were illustrated, and the systematic conclusions were restricted, since only three sera were used to establish the relationships among the various extant genera. The implications that this earlier study had for the systematics of the brachiopods prompted us to conduct a detailed investigation using a more robust immunological distancing approach.

Immunological distance measurements have frequently been used in taxonomic investigations, either using whole organism extracts (Olsen-Stojkovich *et al.* 1986; Price *et al.* 1987) or purified macromolecules (Sarich and Wilson 1967; Lowenstein *et al.* 1981; Lowenstein 1985). The technique involves the preparation of antisera against each taxon studied and reciprocal determinations of all sera against all taxa. In interpreting immunological distance, the technique assumes that the rate of evolution averaged over a large number of antigenic sites is uniform enough to give an accurate portrayal of the evolutionary branching pattern of the groups examined; for serum proteins it has been demonstrated that immunological distance closely parallels protein evolution (e.g. Maxon and Maxon 1979). In addition, within the cancellothyrid genus *Terebratulina* (which is used in this

study) there is excellent congruence between genetic (Cohen *et al.* 1991) and both immunological (Collins *et al.* 1988) and morphological (Cohen *et al.* 1991) data.

The immunological approach is particularly useful for groups such as the brachiopods, where live sampling is only rarely possible. By isolating protected macromolecules (intra-crystalline skeletal glycoproteins), sampling of spirit-stored and dried museum specimens was possible, greatly extending the range of available material. More significantly, *fossil* organic matter isolated from Pleistocene and Pliocene skeletons could also be screened immunologically (Collins *et al.* in press). If it is possible, using immunological distances, to establish a phenogram for Recent brachiopods, this could then be used as a benchmark against which to compare the pattern of reactions of fossil extracts (when tested with the same range of sera), to assess the quality of preserved molecular information (Collins *et al.* in press).



TEXT-FIG. 1. *a*, systematic sub-division of the Terebratulida based on the Treatise (Williams *et al.* 1965). *b*, modifications of the Terebratulida by the inclusion of two new post-Treatise superfamilies proposed by Cooper (1973, 1981).

A total of nine brachiopod antisera were prepared against skeletal glycoproteins. Although the taxonomic distribution of the genera investigated has been dictated primarily by the availability of sufficient quantities of material for antiserum preparation, it has been possible to include taxa which represent all major groups of living articulate brachiopods. Not surprisingly, the number of genera available from each group closely reflects their relative abundance in Recent brachiopod faunas. Thus, five genera were available from among the long-looped terebratulids (which dominate present-day faunas), four of which were assigned to two families of the Superfamily Terebratellacea, while the remaining genus was classified within the Superfamily Dallinacea (Text-fig. 1*b*). Three short-looped terebratulids were available, representing two discrete families which, depending upon interpretation, represented either one (Text-fig. 1*a*) or two (Text-fig. 1*b*) discrete superfamilies. The rhynchonellid genus *Notosaria* was a convenient outgroup for the investigation of terebratulid phylogeny. Roughly 10% of all living brachiopod genera are therefore included in this first comprehensive investigation of the biochemical systematics of brachiopods.

MATERIALS AND METHODS

Species and sources used in the immunological investigation are listed in Table 1. Shells were soaked in concentrated NaOCl (12% active chlorine) solution overnight prior to further handling to remove surface contaminants. Additional NaOCl was added for a minimum 48 hours to remove the inter-crystalline organic matrix, and thereby weaken the shell, liberating the fibres of the secondary shell layer (Collins 1986). It was necessary to treat the rhynchonellid *Notosaria* for a week before shell softening was complete. The fibres were isolated from the remainder of the shell material as previously described (Collins *et al.* 1988) and exhaustively rinsed in double-distilled water prior to freeze drying.

TABLE 1. Species, with localities, used in the immunological distance study.

Taxon	Locality	Prep.	Abbrev.	Serum
Terebratulidae				
<i>Waltonia</i> (<i>Terebratella</i>) <i>inconspicua</i> (Sowerby)	Christchurch, N. Zealand	Fibre	Wi	K5040
<i>Neothyris lenticularis</i> (Deshayes)	Foveaux Strait, N. Zealand	Protein	NL	427
Dallinidae				
<i>Dallina septigera</i> (Lovén)	Hebridian Rise, Scotland	Fibre	Ds	K5007
Kraussinidae				
<i>Kraussina rubra</i> (Pallas)	Southern Tip, S. Africa	Fibre	Kr	801
<i>Megerlia truncata</i> (Gcmlin)	Corsica, Mediterranean	Fibre	Mt	K5053
Cancellothyridae				
<i>Terebratulina retusa</i> (L.)	Firth of Lorn, Scotland	Powder	Tr	K4962
Terebratulidae				
<i>Liothyrella neozelandica</i> (Thomson)	Foveaux Strait, N. Zealand	Fibre	Ln	802
<i>Gryphus vitreus</i> (Born)	Corsica, Mediterranean	Powder	Gv	803
Rhynchonellida				
<i>Notosaria nigricans</i> (Sowerby)	Christchurch, New Zealand	Fibre	Nn	K5038

Intra-crystalline macromolecules were isolated from the secondary layer fibres by de-mineralization in 20% wt/vol disodium ethylene diamine tetraacetic acid (EDTA, pH 8), and the EDTA was subsequently removed by ultra-filtration across an Amicon YM 5 or 10 filter (5 or 10 kD). This treatment yielded approximately 6 mg of water-soluble organic matter per 20 g of fibre preparation.

Special treatments were applied to three samples. For *Gryphus vitreus* it was necessary to use shell powders since secondary layer fibres could not be isolated (this genus develops a tertiary shell layer), *Megerlia truncata*, for which little material was available, was dialyzed against EDTA using the technique of Weiner and Lowenstam (1980), and for *Neothyris lenticularis* a single protein (45 kD) cut from a sodium dodecyl sulphate polyacrylamide gel was used for immunization.

Antisera were prepared using 500 µg aliquots of sample immunized subcutaneously into New Zealand white rabbits according to the following schedule. Primary immunization with Freund's complete adjuvant, followed by three secondary injections with incomplete adjuvant at two to three week intervals, with bleeds after the second and third booster immunizations. Antisera were stored with 0.002% NaN₃ in aliquots at -20 °C.

The IgG fraction of each antiserum was prepared using a crude ammonium sulphate precipitation technique. Saturated (NH₄)₂SO₄ was added drop by drop to serum on ice to final volume of 50%. The serum was left for 30 minutes at 4 °C and then centrifuged at 14000 rpm for 10 minutes. The supernatant was carefully pipetted off and the pellet re-suspended in Tris buffered saline (20 mM Tris, 0.9% wt/vol NaCl, pH 7.5; TBS).

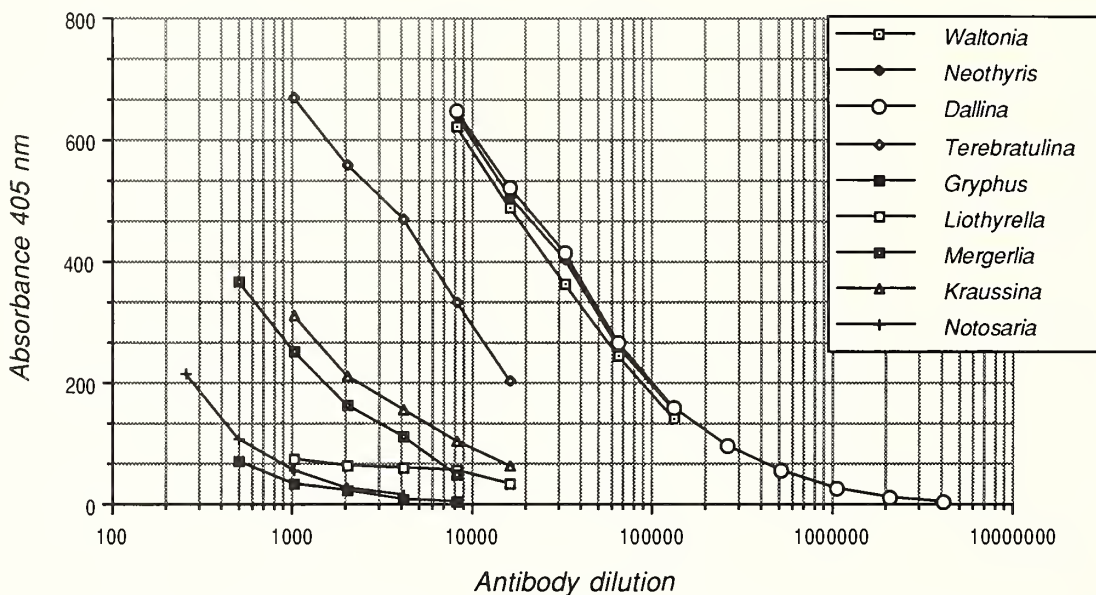
Crude antigen preparations for the immunological assay were produced by dissolving a slight excess of shell fibre (or powder) preparation in 20% wt/vol EDTA (a ratio of 0.046 g fibre/1 ml EDTA), and then centrifuging to remove the residual undissolved carbonate.

An enzyme-linked immunosorbent assay (ELISA; Harlow and Lane 1988) was used to measure immunological distances among taxa. Both antigen (crude EDTA extract) and homologous antiserum were used for all taxa examined, and all antigen-antibody combinations were produced. 10 µl of each crude antigen solution, diluted to 100 µl in 20% wt/vol EDTA, was pipetted onto the microtitre plate which was then incubated at 37 °C for 90 minutes. Unbound antigen was washed away by rinsing three times with washing buffer (TBS to which had been added 0.05% wt/vol of the ionic detergent Tween 20). The wells were blocked for 30 minutes with 2% wt/vol gelatin diluted in TBS. Antisera diluted in 0.2% wt/vol gelatin/TBS/Tween 20 were added to given wells and incubated overnight at 4 °C for 1.5 hours at 37 °C, following which any unbound material was washed away. Alkaline phosphatase labelled goat-anti-rabbit-affinity purified IgG (GAR-AP, Sigma) diluted 1:5000 in gelatin/TBS/Tween 20 was added to the wells for 1 hour at 37 °C after which the wells were rinsed five times with TBS/Tween, once with TBS and then allowed to stand for 2 minutes with phosphatase substrate buffer (pH 9.2), prior to the addition of disodium p-nitrophenyl phosphate (Sigma). After 15 minutes the reaction was stopped by the addition of 50 µl of 1 M NaOH, and the absorbance

at 405 nm of the wells read immediately with a Titretek Multiskan Plus, automated plate reader. The extent of colour development is proportional to the amount of first antibody bound.

Immunological distance was calculated using the formula $ID = 100 \times \log_{10} (100/\Delta)$, where Δ is the mean reciprocal % cross-reactivity (homologous antigen reactivity = 100%; see Table 2). These distances were obtained from the linear regions of semi-logarithmic binding curves plotted using a series of antibody concentrations for each combination of antigen and antibody (Text-fig. 2). Reciprocal distances were averaged for each combination and means of duplicates were used for clustering.

Tree diagrams were constructed either using the method of UPGMA (Sneath and Sokal 1973) or Fitch and Margoliash (1967), as represented by FITCH in the program package PHYLIP, written by Joseph Felsenstein (University of Washington, Seattle).

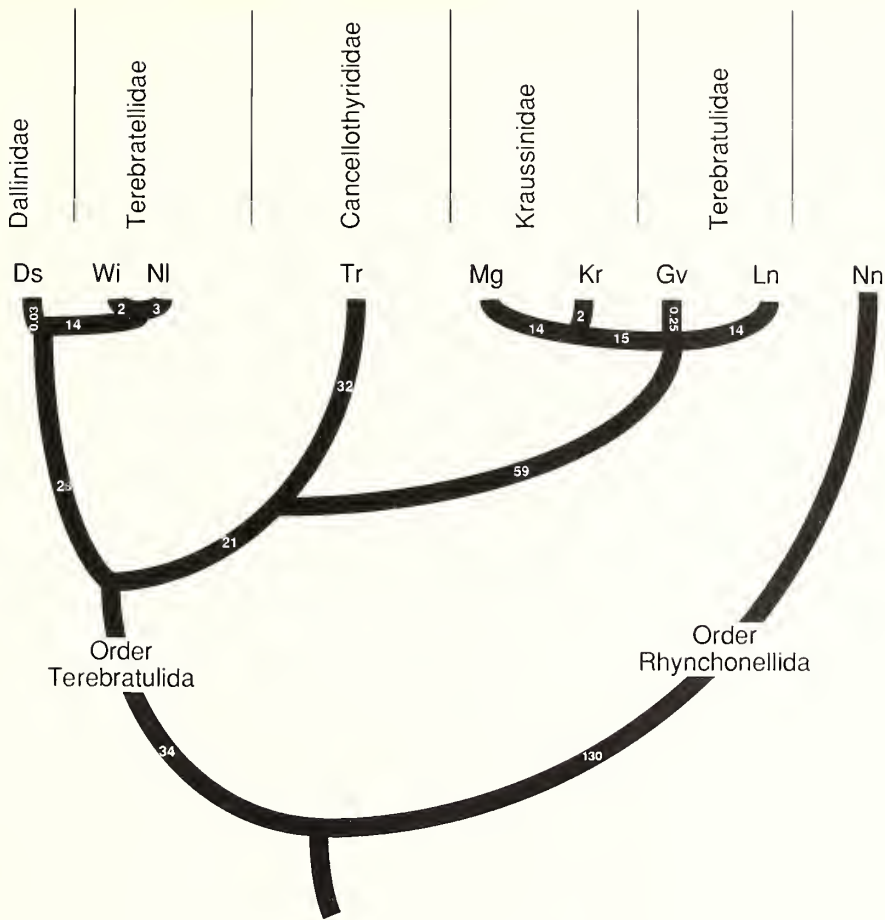


TEXT-FIG. 2. Immunological binding curves. A series of dilutions of the antiserum raised against *Dallina*, tested against all nine antigens. Immunological distance (ID) between species is 100 times the log of the antiserum dilution required to give the same binding for two different species. ID can be determined directly from the linear portions of the binding curves.

RESULTS AND DISCUSSION

Taxonomic framework

In the brachiopod Treatise, the Order Terebratulida was divided into two superfamilies, the long-looped Terebratellacea and the short-looped Terebratulacea. A simplified graphical representation of the Treatise classification down to family level is shown in Text-figure 1a. The classification is based entirely on comparative morphology, and the graphical representation should not be confused with the phenograms used to portray the immunological data. The 'clustering' unit (i.e. vertical axis) is taxonomic hierarchy for the representation of the Treatise classifications, while for the immunological data it is a numerical scale reflecting the degrees of reactivity of the various antisera. To emphasize this point, the analyses of immunological data are shown with the most closely related taxa at the top (i.e. the immunological distance between clusters increases downwards; Text-fig. 3), while the morphological interpretation is shown in the reverse orientation with the lower levels of the taxonomic hierarchy (i.e. families, genera) at the bottom and orders, etc. at the top (Text-fig. 1).



TEXT-FIG. 3. UPGMA phenogram of the immunological distances of nine genera of articulate brachiopods (data from Table 2).

There have been a number of suggested modifications to the Treatise classification some of which have been incorporated into Text-figure 1*b*. The major complication with such modified schemes is that they only deal with relatively few genera, and may leave many unanswered questions about the authors' intended taxonomic assignments, if any, for taxa not discussed. The problem can be circumvented in this paper by including only those groups for which immunological data are currently available. This involves two new superfamilies which have been proposed by Cooper (1973, 1981) and which, in effect, subdivides the two terebratulid superfamilies listed in the Treatise.

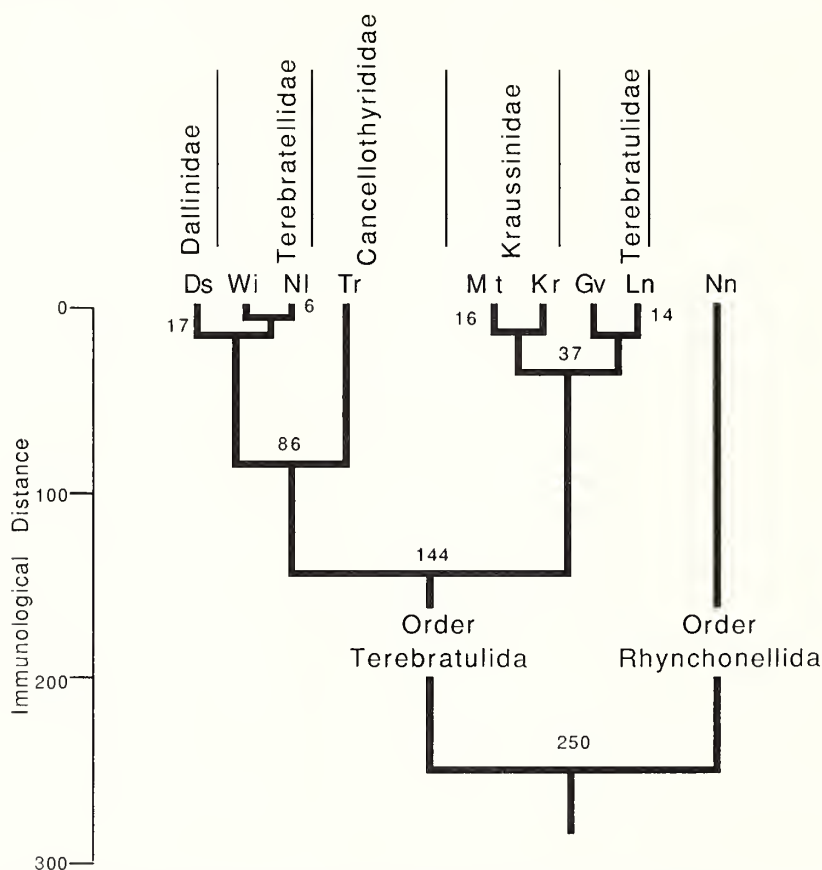
Immunological distances

Immunological distances among genera of the order Terebratulida are presented in Table 2 and the UPGMA and Fitch-Margoliash dendrograms based on this data set are given in Text-figures 3 and 4.

At one extreme, the outgroup rhynchonellid *Notosaria nigricans* was the least reactive with all eight terebratulid antisera, and hence was well separated from the terebratulids in both phenograms (Text-figs 3 and 4). At the other extreme, all confamilial genera clustered together in both forms of analysis (e.g. *Megerlia* with *Kraussina*, *Gryphus* with *Liothyrella*, and *Neothyris* with *Waltonia*;

TABLE 2. Immunological distances among the articulate brachiopods from ELISA of intra-crystalline macromolecules. Distances represent means of reciprocal distances obtained from binding curves. See Table 1 for species abbreviations.

	Wi	Ds	NL	Tr	Gv	Li	Mt	Kr	Nn
<i>Waltonia inconspicua</i>	0	15	6	100	169	177	204	117	301
<i>Dallina septigera</i>		0	18	77	118	129	154	170	168
<i>Neothyris lenticularis</i>			0	88	156	149	130	132	239
<i>Terebratulina retusa</i>				0	134	70	146	206	253
<i>Gryphus vitreus</i>					0	14	45	15	193
<i>Liothyrella neozelandica</i>						0	34	54	272
<i>Megerlia truncata</i>							0	16	284
<i>Kraussina rubra</i>								0	306
<i>Notosaria nigricans</i>									0



TEXT-FIG. 4. Fitch-Margoliash phenogram of the data from Table 2. Note that while the overall topology is similar to Text-figure 3, the cancellothyrid lineage (*Terebratulina*) arises from the terebratulid, and not the TLD, lineage.

Text-figs 3 and 4). These results, at the highest and lowest level of the taxonomic hierarchy investigated, are entirely consistent with established morphology-based brachiopod systematics, and reinforce our contention that intra-skeletal macromolecules are an important source of phylogenetic information (Collins *et al.* 1988).

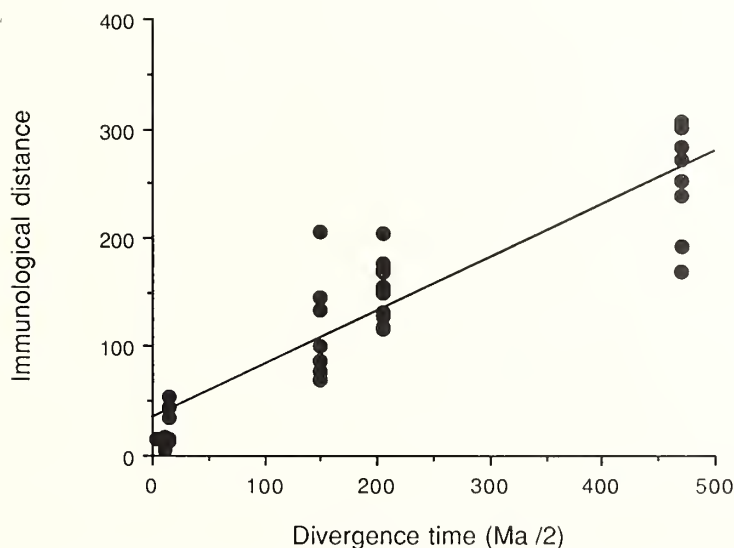
Within the terebratulids, the immunological distances distinguish three main clusters (Text-figs 3 and 4). The novel aspect of these three main clusters is that they do not coincide with the long- and short-looped stocks which, as mentioned above, currently represent the primary subdivisions of the terebratulids. Instead, two represent respectively the Cancellothyrididacea (raised to superfamily status by Cooper 1973) and a sub-group of the Terebratulacea (the so-called TLD group of Collins *et al.* 1988). The third is more heterogeneous, including both a long-looped family (the Kraussinidae) and short-looped superfamily Terebratulacea.

The fact that the three-way clustering pattern is confirmed by two different methods of analysing the data (Text-figs 3 and 4), and is based on fully reciprocal immunological distances, confirms that this is an accurate reflection of the phylogenetic relationships among living terebratulids.

Plotting the immunological distances of the major nodes against estimated divergence times (Table 3) reveals a strong correlation (Text-fig. 5). However, given that there is no universal 'molecular evolutionary clock' (e.g. Britten 1986), it is necessary to put this apparent correlation into context.

TABLE 3. Estimated divergence time of major branches used in regression of ID against range.

Divergence	mcan ID	Time (Ma)	Rationale (first occurrence of...)
No divergence	0	0	
Wi from NL	6	12	genus <i>Waltonia</i>
Mt from Kr	16	3	genus <i>Kraussina</i>
Li from Gv	14	15	genus <i>Liothyrella</i>
DI from Wi, NL	16	15	subfamily Neothyridinae
Mt, Kr from Li, Gv	37	15	family Kraussinidae
Tr from DI, Wi, NL	100	150	genus <i>Terebratulina</i>
Mt, Kr, Li, Gv from DL, Wi, NL	163	205	subfamily Terebratulinae
Nn from others	295	470	Order Spiriferida (ancestral to the Terebratulida)



TEXT-FIG. 5. Plot of immunological distance against range. Divergence times are estimated from the ages given in Table 3.

The divergence times (listed in Table 3) used for the analysis are based on the first appearance of the most recent probable ancestor, but these are not always well defined, and are subject to significant change as continuing investigation of fossil brachiopods extends or reduces the known range of taxa. In addition, although the approach of using polyclonal antisera against a large number of different determinants will generate an averaged clock speed, which is beneficial, the structure of individual antigenic determinants is not known. The immunological determinants of the glycoproteins are believed to be mainly sugar moieties (due to their sensitivity to periodate and their insensitivity to proteinase K treatments; Collins *et al.* in press), the production of which is controlled by complex pathways, of whose evolutionary patterns we remain ignorant.

Evolution of the Order Terebratulida

The Order Terebratulida, which is first recorded from the Lower Devonian, is characterized by the possession of a distinctive internal skeleton, 'the loop'. The traditional interpretation of evolution within this order is of considerable 'experimentation' with the internal skeleton in the early Devonian. The period of diversification was relatively short (e.g. Stehli 1965; Rudwick 1970; Williams and Hurst 1977), with two distinct lineages diverging in the late Devonian, giving rise to the present-day Terebratulacea (short loop) and Terebratellacea (long loop).

The serotaxonomic data clearly indicate that this interpretation is in considerable need of revision. Assuming the minimum age for diversification of the rhynchonellid and terebratulid lineages is approximately 470 Ma at the first appearance of the order Spiriferida (believed to be ancestral to the Terebratulida), then the great immunological distances between this primary division and subsequent diversification suggests that surviving lineages diversified considerably later than the Devonian.

The immunological data would suggest that the three modern-day lineages identified in this study (TLD terebratellaceans, the cancellothyrids, and the 'terebratulaceans', the latter including the Kraussinidae) diverged from each other at around the same time (Text-figs 3 and 4). An early Mesozoic diversification is implied by the immunological data, which is consistent with the appearance of the first terebratellacean and terebratulacean genera in the Upper Triassic, and the earliest cancellothyrids from the Middle to Upper Jurassic (Muir-Wood *et al.* 1965).

The three major lineages have subsequently undergone different patterns of evolution. The most morphologically conservative have been the cancellothyrids, which have changed very little since the late Jurassic, and which consequently have the largest and older surviving terebratulid genus *Terebratulina*, surely a case for revision?

The small immunological distances between the three members of the TLD cluster imply a high degree of relatedness, which runs contrary to the assumption that members of this lineage diversified as early as the Upper Cretaceous (Muir-Wood *et al.* 1965). Conversely, the immunological distances which separate the Kraussinidae from the Terebratulidae are greater than is anticipated from a geological record for the former family which extends back only into the Miocene.

The clustering of *Macandrevia*, previously included in the Dallinidae (Muir-Wood *et al.* 1965), or Laqueidae (Richardson 1975), within the 'kraussinid' group (Text-figs 3 and 4) illustrates the limited value of loop morphology for familial assignment. The value of the loop as a taxonomic character is further reduced when (as is common in fossil samples) its ontogeny is difficult to decipher. The serological data suggest a much closer relationship between *Dallina* and the Terebratellidae than a Cretaceous diversification would imply. It is clear that future studies will have to determine whether the accepted familial assignments of Cretaceous genera are justified, with their added implication that both the laqueid and terebratellid lineages (*sensu* Richardson 1975) can be traced back to the Cretaceous.

The phylogeny of the Kraussinidae has recently been discussed by Brunton and Hiller (1990). If the lineage also includes the Megathyrididae, as suggested by our previous study (Collins *et al.* 1988), and expected from current classification, the divergence of this lineage would be placed in the late Mesozoic, which more closely corresponds with the immunological distances observed. The major revelation arising from the immunological data, although anticipated in our earlier study

(Collins *et al.* 1988), is not the divergence time of the kraussinid cluster, but its origin. The immunological data clearly indicate that the lineage is derived, not from the long-looped terebratellaceans (TLD group), but from the short-looped (terebratulacean) stock. In reviewing the phylogeny of the kraussinids, Brunton and Hiller (1990) justifiably comment that our preliminary results (Collins *et al.* 1988) linking the kraussinids to the terebratulaceans were surprising, given that there is no obvious kraussinid-like ancestor within this lineage. However, additional antisera raised for this investigation, against *Kraussina*, *Megerlia*, *Liothyrella*, and *Gryphus*, all confirm the original finding. This result has major taxonomic implications, not only for the classification of the kraussinids, but for the significance of the loop as a subordinal taxonomic character.

Taxonomic Implications

Immunological data cannot on their own determine the taxonomic relationships of terebratulid brachiopods, because only Recent taxa are involved in the immunological distance experiments. The data only relate to the phylogenetic relationships of the families to which the included genera are assigned, and these assignments may be incomplete or wrong (e.g. *Macandrevia*; Collins *et al.* 1988). However, the immunological study highlights relationships which contradict current morphological classifications.

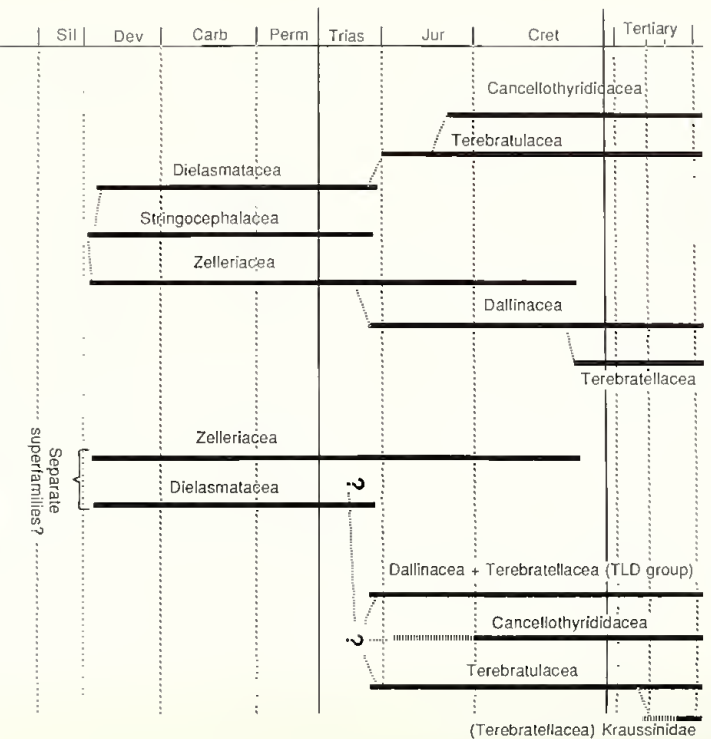
The simplified cardinalia and distinctive loop morphology of the cancellothyrids make this the most homogeneous of the extant terebratulid lineages.

The TLD terebratellaceans are characterized by supporting hinge plates on the median septum, which distinguishes these terebratellaceans from the 'aberrant' genus *Macandrevia*, but this latter organization is also seen in some Palaeozoic terebratulids and in other articulate brachiopod orders. The loop, which is best developed within this group, has previously been cited as the major discriminatory feature in the terebratulids (e.g. Stehli 1965). However, ontogenetically, there is a strong relationship between long- and short-looped forms. The earliest stages in the development of the descending branches of the calcareous loop up to their fusion with the median septum are the same for all three extant lineages. Elliott (1953, 1957) notes that the first-formed calcareous support for all modern long-looped brachiopods (with the exception of *Argyrothea*) always includes a dorsal median septum. Of the Palaeozoic superfamilies of terebratulids believed to be ancestral to modern forms, all contain genera which possess median septa, but there is no clear evidence for the involvement of the septum in the ontogeny of the loop in either the Stringocephalacea or Zeileriacea. If in these two superfamilies a long loop was derived simply by anterolateral growth of a short dielasmatacean-like loop, then the role of the median septum in all modern long-looped lineages is significant. The fixing of *one* novel character, a link between an acceleration in the time and rate of growth of the median septum coincident with that of the descending branches was probably all that was necessary to pave the way for the Mesozoic and Cenozoic diversifications (Text-fig. 6).

Immunological distances provide an important new perspective on terebratulid evolution, and pose problems for current morphologically-based taxonomy. Morphological taxonomy of a group with such a 'simple' skeleton is prone to error, yet molecular taxonomy is generally inapplicable to a predominantly fossil group. Therefore, a major taxonomic revision of this order appears inevitable, and it should proceed as a rigorous re-analysis of skeletal ontogeny and morphology in the light of a more widespread molecular investigation.

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Traditional Interpretation

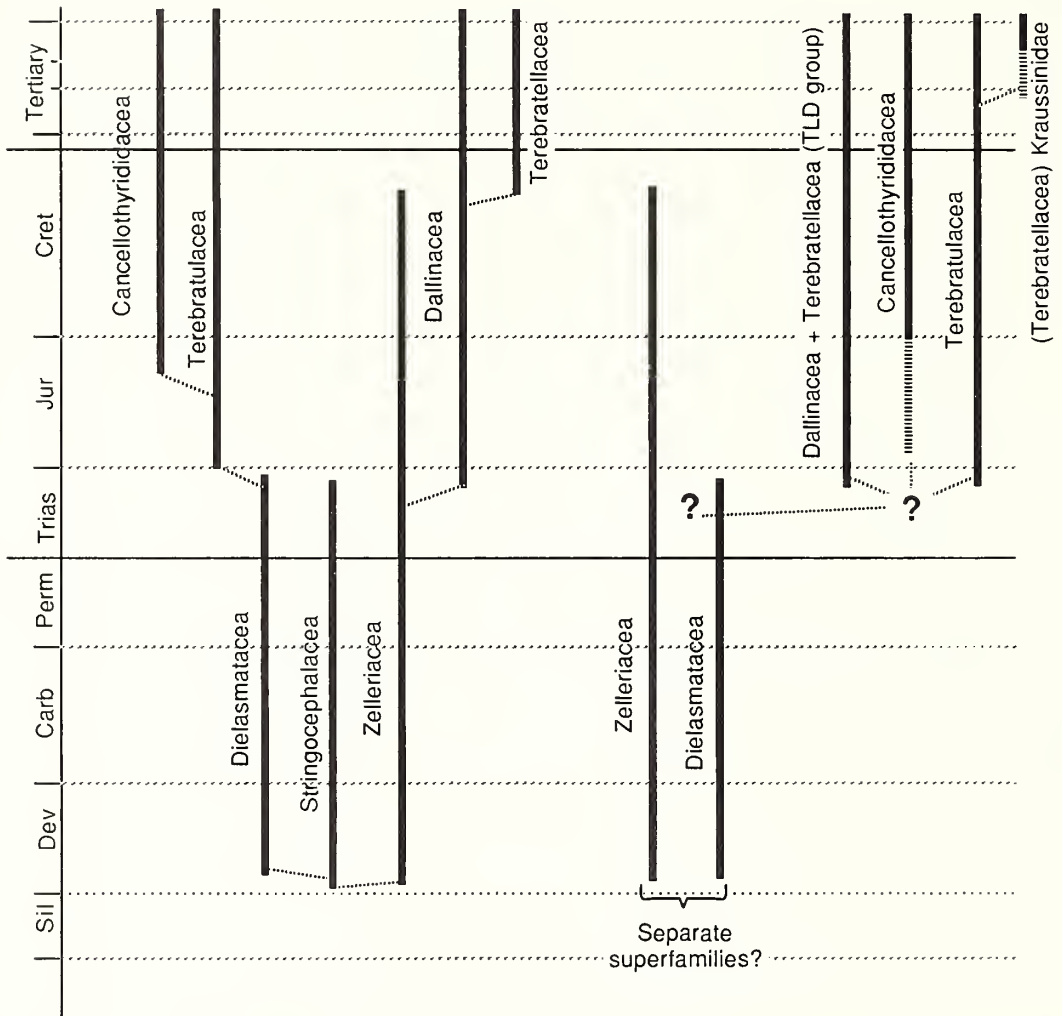
Interpretation based
on serotaxonomy

TEXT-FIG. 6. Terebratulid phylogeny (after Williams and Rowell 1965; Williams and Hurs 1977) reinterpreted in the light of the serotaxonomic data.

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Traditional Interpretation

Interpretation based
on serotaxonomy

TEXT-FIG. 6. Terebratulid phylogeny (after Williams and Rowell 1965; Williams and Hurst 1977) reinterpreted in the light of the serotaxonomic data.

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FEEDING STRATEGIES IN GRAPTOLIDS

by SUSAN RIGBY

ABSTRACT. The progressive loss of stipes through the Ordovician and the appearance of uniserial forms in the Silurian mark obvious changes in graptoloid morphology through time. However, several features of graptoloids are shown here to have remained remarkably constant. These include stipe width and the number of thecae per cm. The number of zooids in an entire colony (assuming a one-to-one ratio with the thecae) changes abruptly at the Ordovician–Silurian boundary but the range of zooid numbers remains the same. The feeding areas of graptoloids, and the intensities with which they fed have been measured, assuming that graptoloids rotated as they moved through the water. The mean and range of feeding intensity remained constant through time although the total number of zooids changed. Silurian curved monograptids plot in the same place as inclined biserial forms and tetragraptids on a feeding intensity–area graph. Multiramous colonies in both the Ordovician and Silurian plot in the same place. Scandent biserial forms plot with straight monograptids. It is postulated that graptoloids with low feeding intensities lived in areas of low food availability. High intensity feeders would have lived where food was more abundant. Colony size (measured as total number of zooids) might have related to the dependability of food supply.

THERE are obvious changes in graptoloid morphology through time. Early Ordovician forms with many stipes gave rise to forms with progressively fewer stipes, although a multiramous component to the fauna was almost always present. Monograptids first appeared close to the Ordovician–Silurian boundary, and came to dominate Silurian faunas. They gave rise to new types of multiramous graptoloids, produced by cladal generation rather than by dichotomy.

This constant change in colony form allows accurate biostratigraphical correlation of the Ordovician and Silurian periods. The reasons for the change are unknown. Bates and Kirk (1985) postulate that the initial radiation of planktonic graptoloids resulted in ‘...increased automobility, giving access to the higher and more food rich layers of the water’. Later reductions in the number of stipes are suggested to have prevented graptolites from becoming tangled with one another in the crowded Palaeozoic seas. Rickards (1975) suggests that the initial reduction in stipes reduced the weight of the colony. Later changes in the orientation of the stipes may have served to remove the delicate proximal end from turbulent surface waters.

It would be expected that radical changes of form would mirror changes in life habit. However graptoloids were colonial. Changing the colony form would not necessarily have changed the form of the zooids. A simple change in ‘building instructions’ to a colony would have resulted in radical changes to the overall form, but the colony would have survived if this form was in any way advantageous. This contrasts with non-colonial organisms where most mutations to the transcribed DNA are fatal because they affect so many metabolic processes. Thus changes with such serious implications for biostratigraphy as the first appearance of monograptids need not be seen as a response to changes in the environment or in graptoloid life habit.

The graptoloid rhabdosome needed to perform a number of functions for the colony to have survived. Only some of these are known at the present time. One was the need to present a hydrodynamically stable form to the water so that the zooids would not interfere with one another whilst feeding. Scandent colonies needed to remain scandent; horizontal forms needed to retain that orientation. Hydrodynamic needs may also have included including rotation to the colony as it moved through the water (Rigby and Rickards 1989). Another need was to present the zooids to the water in an efficient feeding array for the available food. The methods by which this was achieved in multiramous colonies have been investigated by Fortey and Bell (1987).

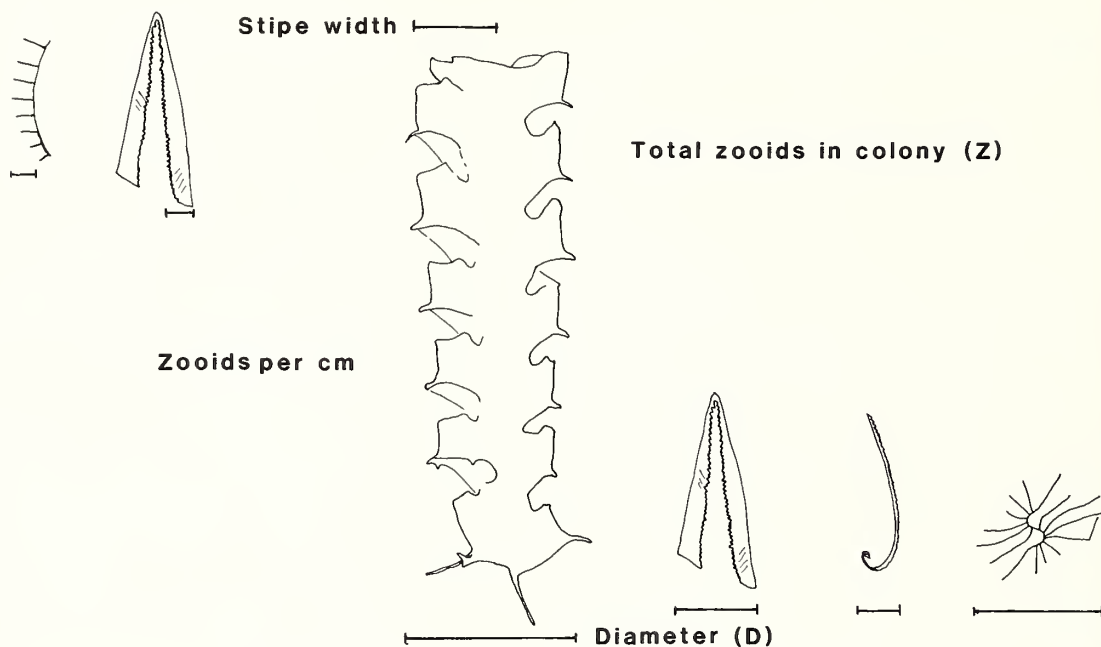
It is important to note that a range of morphologies could have achieved the same result. This

is certainly seen in multiramous colonies, where Silurian forms with curved cladia achieved a high coverage of the available area, just like Ordovician forms which were multiramous due to dichotomizing branches (Fortey and Bell 1987).

The purpose of this paper is to explore some aspects of graptoloid morphology which are common to every graptoloid regardless of the number and orientation of the stipes. Changes in these features through time can be compared to overall changes in morphology, to see whether these large scale changes necessarily marked a significant change in life habit.

METHODS

The features (Text-fig. 1) chosen were: (1) number of zooids per centimetre of stipe; (2) stipe width; (3) total number of zooids in the colony (Z); (4) area (A) or diameter (D) of feeding circle; and (5) feeding efficiency (Z/A or Z/D).



TEXT-FIG. 1. Measurements made on graptoloids for this study.

Measurements of zooids per cm stipe width, total number of zooids in the colony, feeding area and feeding intensity were made on the species figured by Elles and Wood (1901–18) in their *Monograph of the British Graptolites*, with the exception of the retiolitids and other forms with skeletal rhabdosomes. Two hundred and forty two species were included. This data set was chosen because it runs from the Tremadoc to the end of the Silurian. Some species have been synonymized, and many more defined since this work was done. Some zonal boundaries have been redefined. However, it remains the only comprehensive view of British graptoloids and so was used in its entirety, without addition or alteration. This should have avoided any changes in bias derived from different interpretations of what constitutes a species which would have resulted in different authors' views had been taken for different zones.

In some cases the drawings and text descriptions were at odds. In these cases the drawings were used as it was necessary to use these for measurements of feeding area. In the case of some multiramous forms, e.g. *Cyrtograptus munchisoni*, graptoloids had to be reconstructed from incomplete figured specimens. In these cases the branching rules used in the fragments of

rhabdosome were followed, and the overall form assumed to have been circular (Bulman 1970). Forty specimens were measured from the original specimens and these values compared with those obtained from the drawings in Elles and Wood (1901–18). There were no significant differences in the readings, with an average discrepancy between the two of 0.5 mm.

The number of thecae per cm is given in species descriptions. It is normally a range, and in these cases the highest value was taken. A rhabdopleuran model was assumed for the graptoloid zooid (Rickards 1975) with one zooid filling one theca. It is possible that a *Cephalodiscus* type strategy might have been adopted, with several zooids for each thecal cup. This would necessitate multiplying the number of thecae by a correction factor.

Stipe width was measured as the distance between the tip of a theca and the dorsal wall of the rhabdosome. It was taken as the maximum width on the drawing of the specimen, or from the width given in the species description if it was apparent that the colony was flattened. It is possible that an exaggerated value was given for some specimens where only flattened specimens have been recovered.

The total number of zooids in the colony was measured from Wood's drawings or taken from the maximum colony length given in species descriptions when this gave a greater value. In these cases the maximum length given was multiplied by the number of thecae recorded per cm. This measurement would obviously have changed continuously as the colony grew. Some species may have continued growing indefinitely, for instance *Monograptus flemingi*, of which there is a specimen in the Sedgwick Museum (A52567) 75 cm long. Other graptoloids would have reached a maximum growth size beyond which they could not physically progress. An example is *Skiagraptus* which narrows distally to a point. As a first order approximation, the maximum length described by Elles, or the length of the specimen drawn by Wood was taken, whichever was longer.

Feeding area was calculated assuming that the colony fed during spiralling motion through the water column (Rigby and Rickards 1989). This is accepted to have been unlikely in all colony forms. However, almost all of the species so far modelled had the capacity to rotate. These include *Pseudoclinacograptus*, *Triaenagraptus*, *Cyrtograptus*, dicellograptids, dicranograptids, hooked and straight monograptids, *Orthodichograptus*, *Trochograptus*, *Dichograptus*, *Loganograptus*, and *Nemagraptus*. Standard orientations were assumed. There is some evidence for these orientations (Rickards and Crowther 1979; Fortey and Bell 1987) and more is emerging from physical modelling. It makes no difference which way up the rhabdosome is assumed to have lived, sicula up (Bates and Kirk 1985 and references therein) or sicula down (Bulman 1964). Each colony would have spiralled through a column of water of unknown length. The area of a circular section through this tube can be measured. The diameter of this circle is given by the width of the colony (Text-fig. 1). The assumption of rotation is crucial; if it did not occur then a circular area of water would have been tapped by few species.

Feeding intensity was measured by dividing the total number of zooids by the area of water from which they must have fed. In Text-figure 6 this is plotted as Z/D , i.e. as the total number of zooids divided by the diameter of the feeding circle. This was done to reduce the range needed to plot the graph which is greatly increased when area is used. The total zooids were divided by the area of feeding circle for all other graphs.

No allowance was made for possible different rates of rotation, or different speeds of movement through the water. These factors cannot at present be defined with any degree of accuracy. Some graptoloids may have achieved larger colonies than those preserved or yet discovered. Post-mortem effects may have distorted the stipe thickness and colony diameter recorded for some species. So all of the number given must be regarded as approximations. They are not presented as highly accurate values but as readings which allow comparison between apparently dissimilar morphologies.

RESULTS

Zooids per cm

The mean number of zooids per cm in Ordovician graptoloids was 11.8. In Silurian forms it was

11.4 cm⁻¹. In both cases the mode is 10 cm⁻¹. Standard deviations are 2.5 cm⁻¹ and 2.9 cm⁻¹ respectively (Text-fig. 2). In effect there is no significant change in these values across the Ordovician–Silurian boundary. The range of values, however, was greater in the Silurian, with a maximum of 28 cm⁻¹, and a minimum value of 1 cm⁻¹. This contrasts with an Ordovician range of 14 cm⁻¹, between 5 cm⁻¹ and 19 cm⁻¹. In the Silurian the greater range is largely due to relatively uncommon or short lived genera such as *Rastrites*.

These values compare with Fortey's (1983) 'average graptoloid' which had 9–10 thecae per cm.

Stipe width

The modal value of stipe width in both Ordovician and Silurian forms is 1.5 mm. The mean rises from 1.8 mm in the Ordovician to 2.2 mm in the Silurian. The standard deviation rises from 1.1 mm to 1.6 mm (Text-fig. 3). These two changes are almost wholly due to the appearance of the genus *Rastrites* in the Silurian. These forms have isolated thecae which can be 18 mm long. When these forms are excluded from the calculation, the mean for the Silurian becomes 1.88 mm and the standard deviation 1.1 mm, effectively the same as Ordovician values. Fortey's (1983) 'average graptoloid' had a stipe 2.2 mm wide.

Total number of zooids in colony

The mean number of zooids in a colony is 171 in the Ordovician, and falls to 95 in the Silurian. The mode falls from 250 to 25. The standard deviation for the Ordovician forms is 205, showing massive variability in colony size. In the Silurian it is 94 (Text-fig. 4). This is a significant difference between graptoloids of different ages.

Feeding diameter

Ordovician feeding diameters range from 1 mm to 640 mm, with a mean of 56 mm and a mode of 2.5 mm. The standard deviation is 10.3 mm. By contrast, the Silurian range is from 0.5 mm to 140 mm, with a mean of 9.7 mm and a mode of 0.25 mm. The standard deviation is 2.1 mm, reflecting the smaller, more clustered distribution (Text-fig. 5). The large number of modal graptoloids in each case make the distributions appear similar. A Spearman's Rank Correlation Coefficient test was applied to the data, using the null hypothesis that there was no correlation between the two frequency distributions. This test was chosen as it is non-parametric and suitable for grouped data (Hammond and McCullagh 1974). The null hypothesis had to be rejected when the correlation between the two distributions was found to be significant at the 0.01 level.

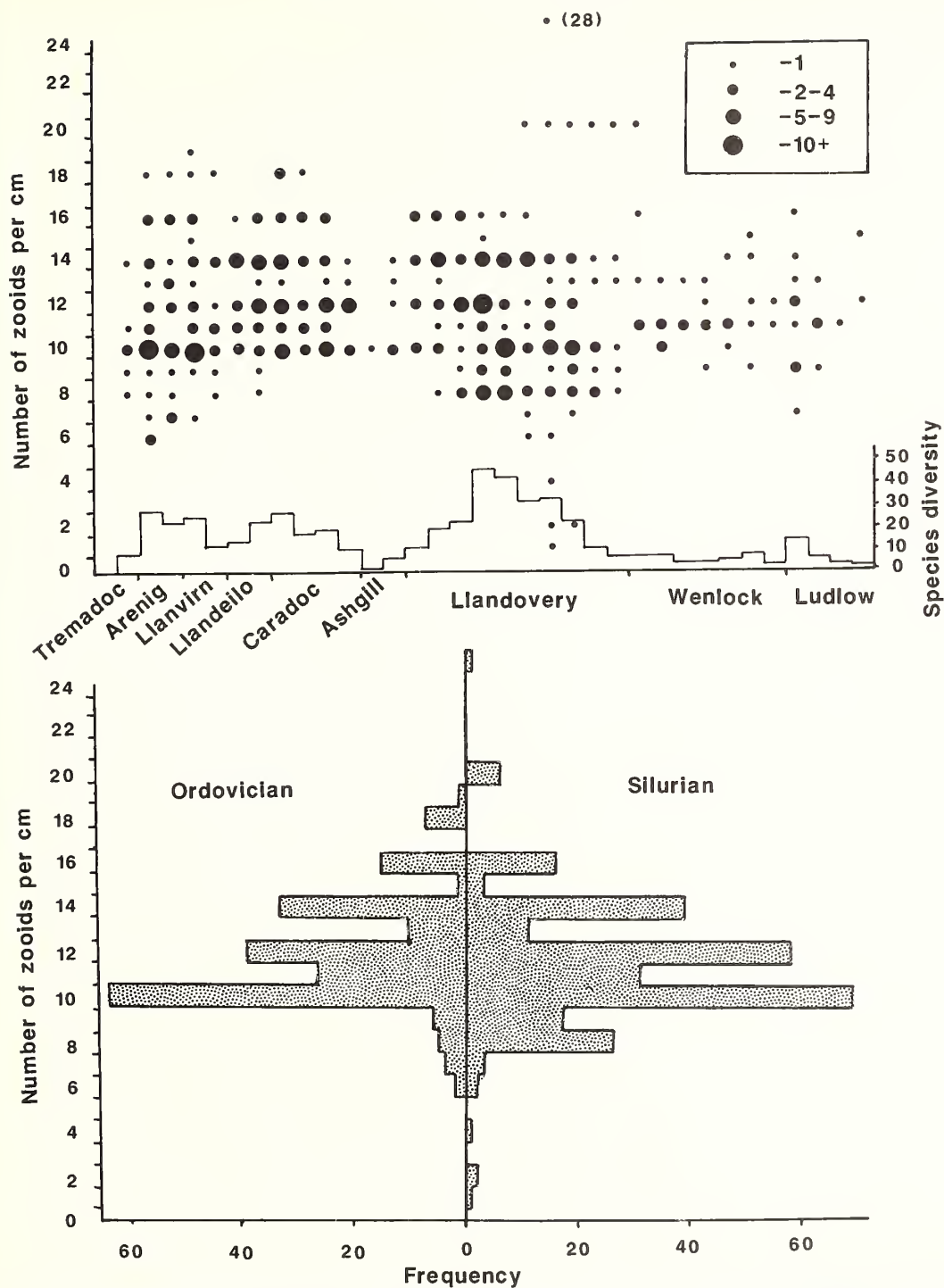
Feeding intensity

The range of feeding intensities shown by graptoloids of both Ordovician and Silurian age is from less than 10 to almost 1500 zooids per diameter cm (informally labelled as $x \text{ cm(D)}^{-1}$). The mean value is 254 cm(D)⁻¹ in the Ordovician and 281 cm(D)⁻¹ in the Silurian. In both cases the mode is 750 cm(D)⁻¹. Standard deviation is 291 cm(D)⁻¹ in the Ordovician and 297 cm(D)⁻¹ in the Silurian (Text-fig. 6). In the light of the enormous range of variation which is present, these differences are negligible. A Spearman's Rank Correlation Coefficient was applied, using the null hypothesis that there was no correlation between the two distributions. This had to be rejected as the data were found to be significantly correlated only at the 0.5 level.

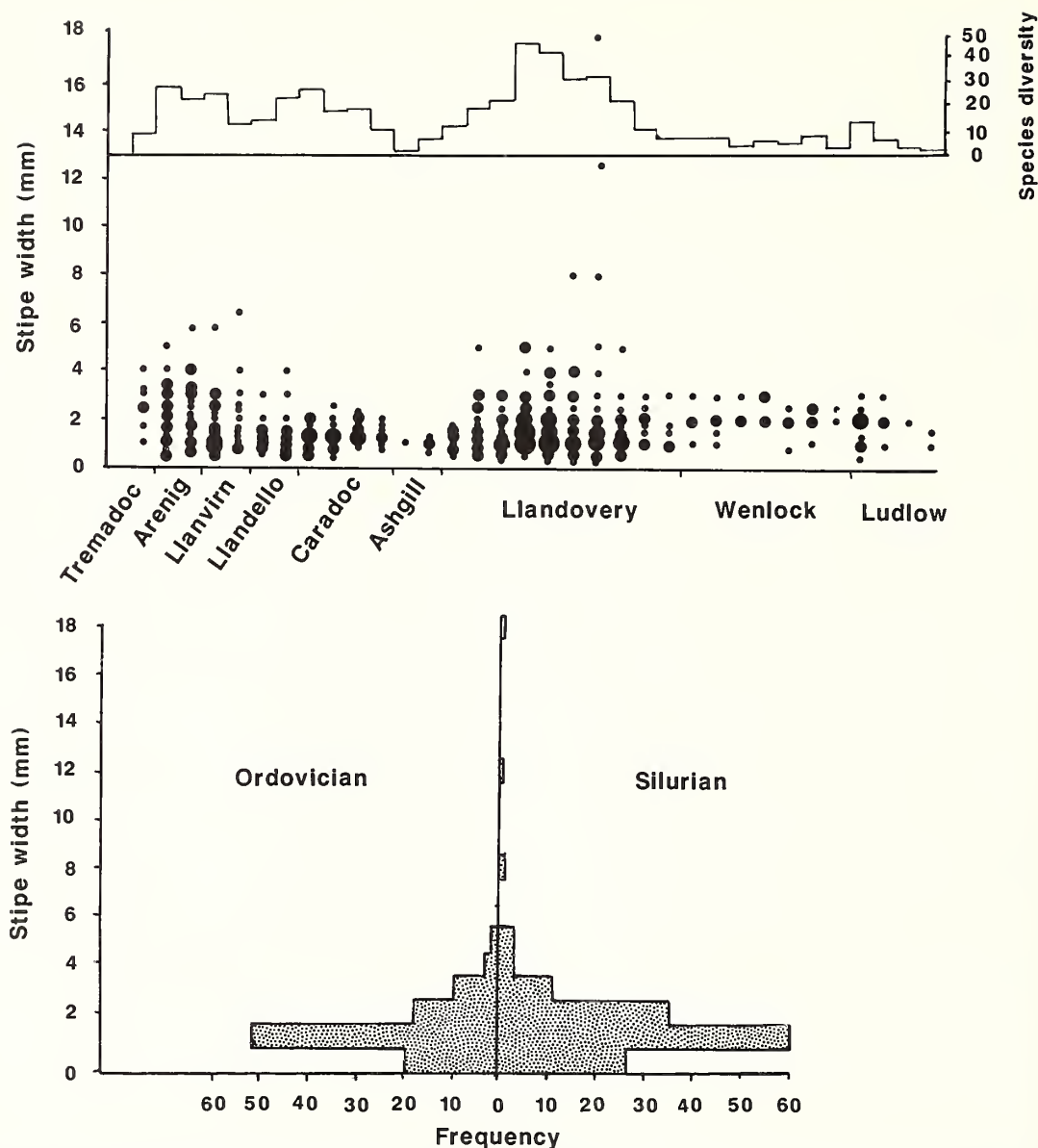
FEEDING INTENSITY – AREA PLOTS

Feeding intensity can be plotted against the area of the feeding circle for each species of graptoloid. The resulting graphs are shown in Text-figure 7. The range of variation is great and log scales need to be used on both axes. This makes it appear that there is a straight line correlation between the two, but this is misleading. The plots are the result of a range of factors and Z/A is not simply correlated with A .

The variables on these graphs are linked in such a way that as A increases, Z/A will tend to



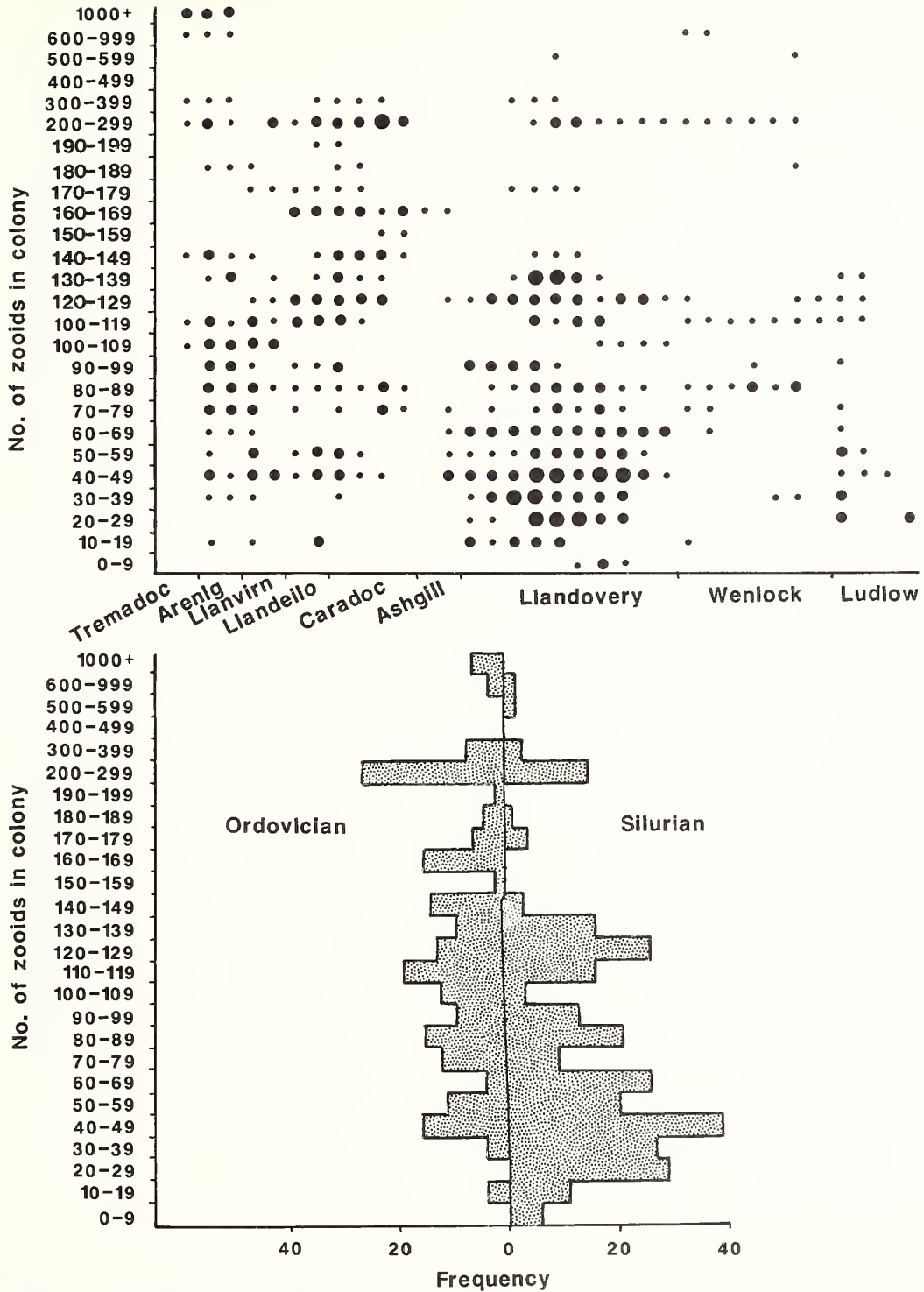
TEXT-FIG. 2. Number of zooids per cm plotted against time. Spot size is proportional to the number of readings in each position. The bar graph represents the same data, on the same y-axis but summarized for the Ordovician and Silurian. Note that a species was counted once for every zone in which it was found. This is true for all of these graphs.



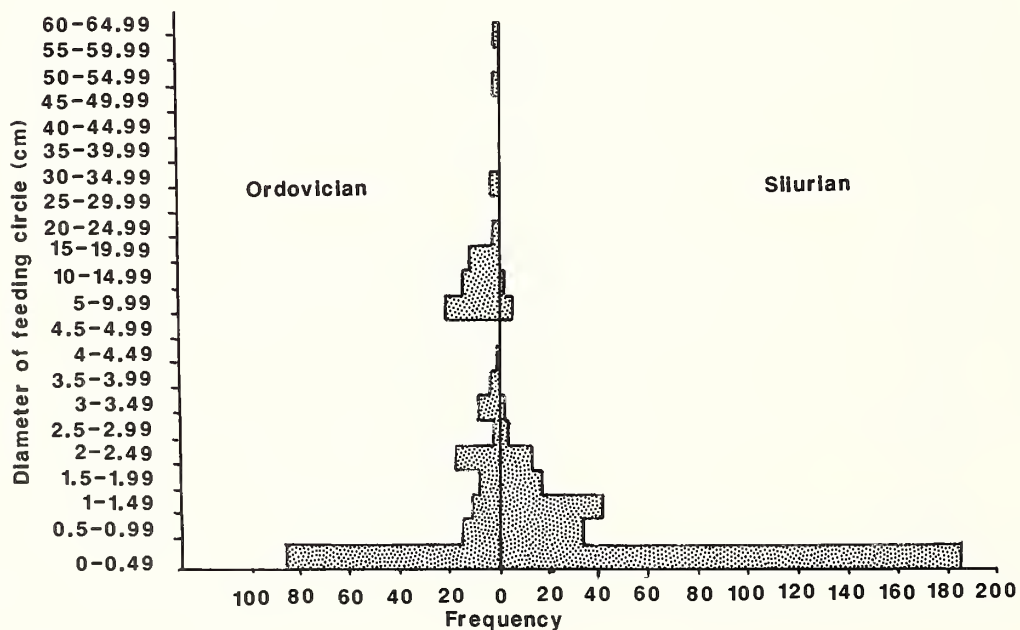
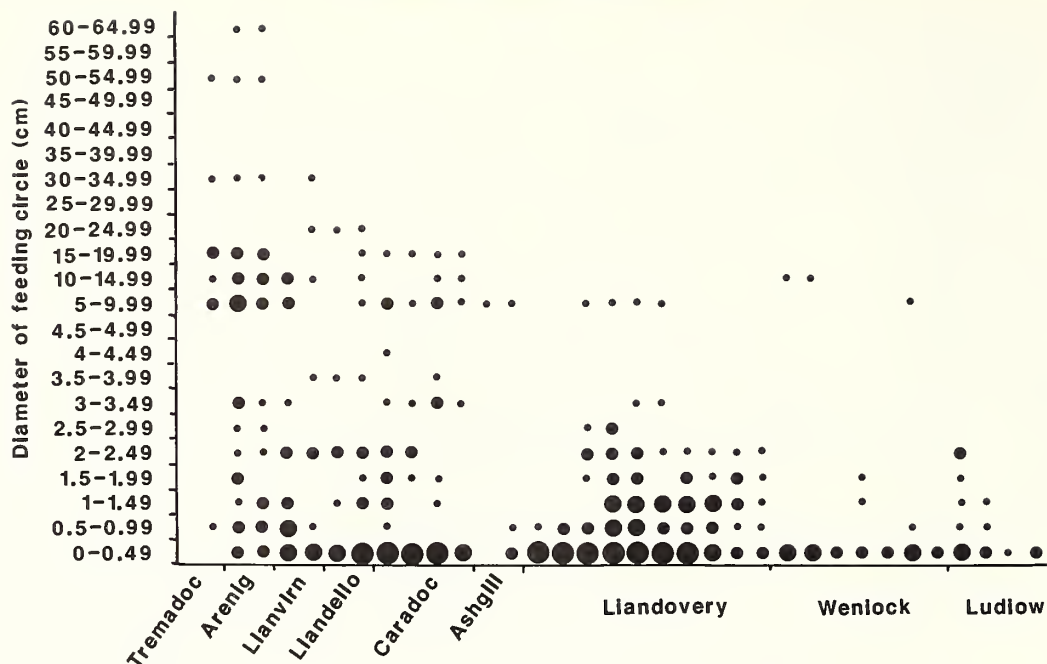
TEXT-FIG. 3. Stipe width plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).

decrease. This contributes to the negative correlation seen on the graphs. However, the correlation between the two variables is not the source of interest of the plots. They should instead be regarded as a crude section through graptoloid morphospace. The variables are plotted separately in Text-figures 5 and 6, but plotting both on the same graph is convenient shorthand.

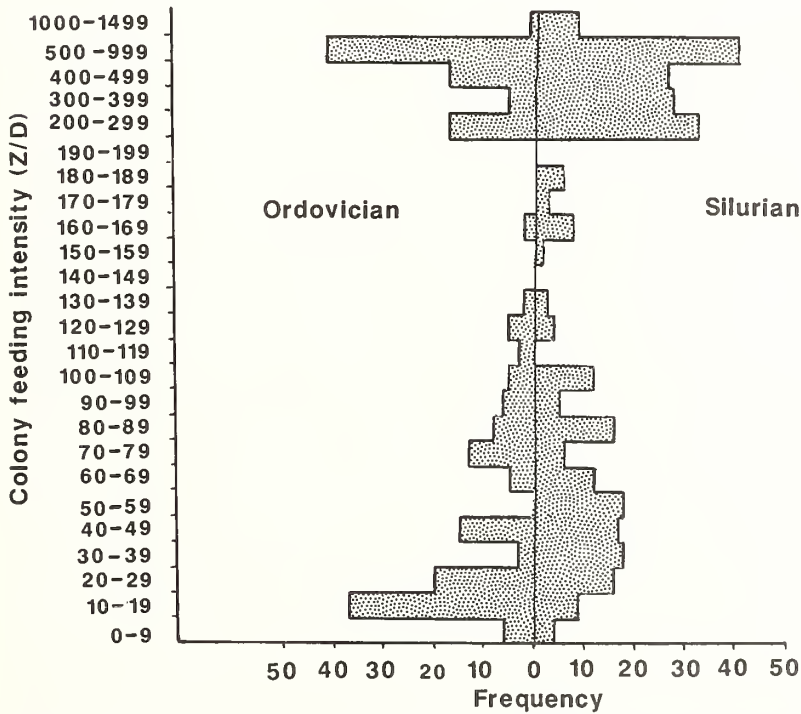
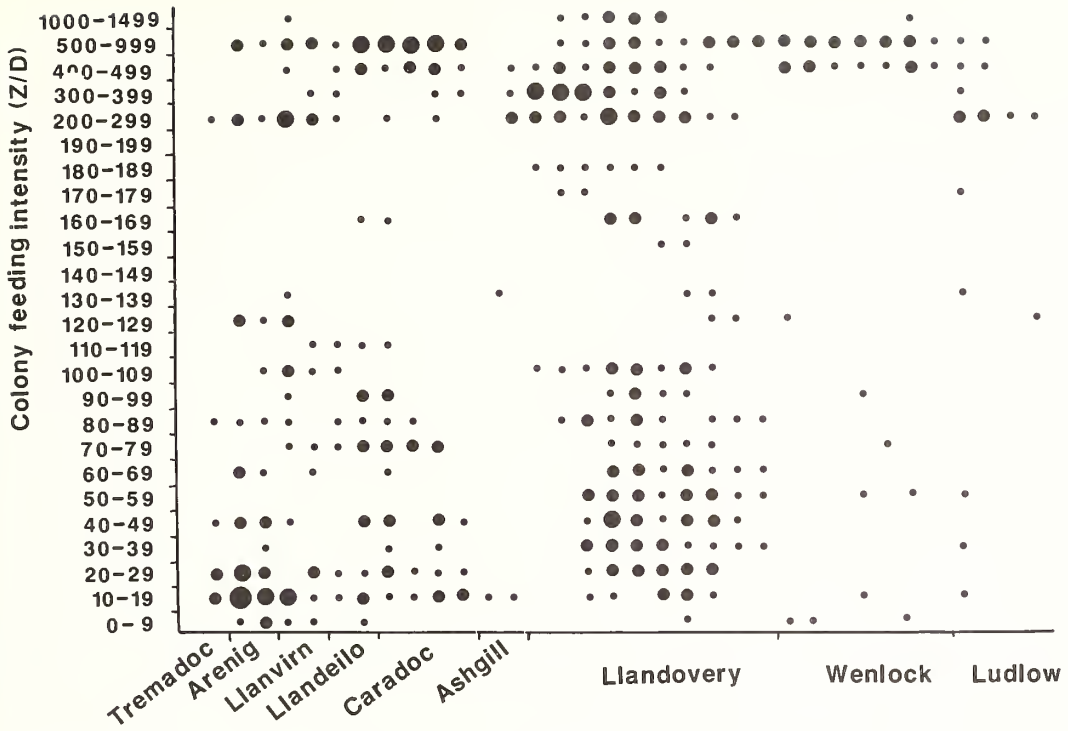
The important result from these graphs is the striking similarity of the Ordovician and Silurian plots. It must be remembered that feeding intensity is a function of several factors, including the total number of zooids in the colony. The mean of this value changes abruptly at the



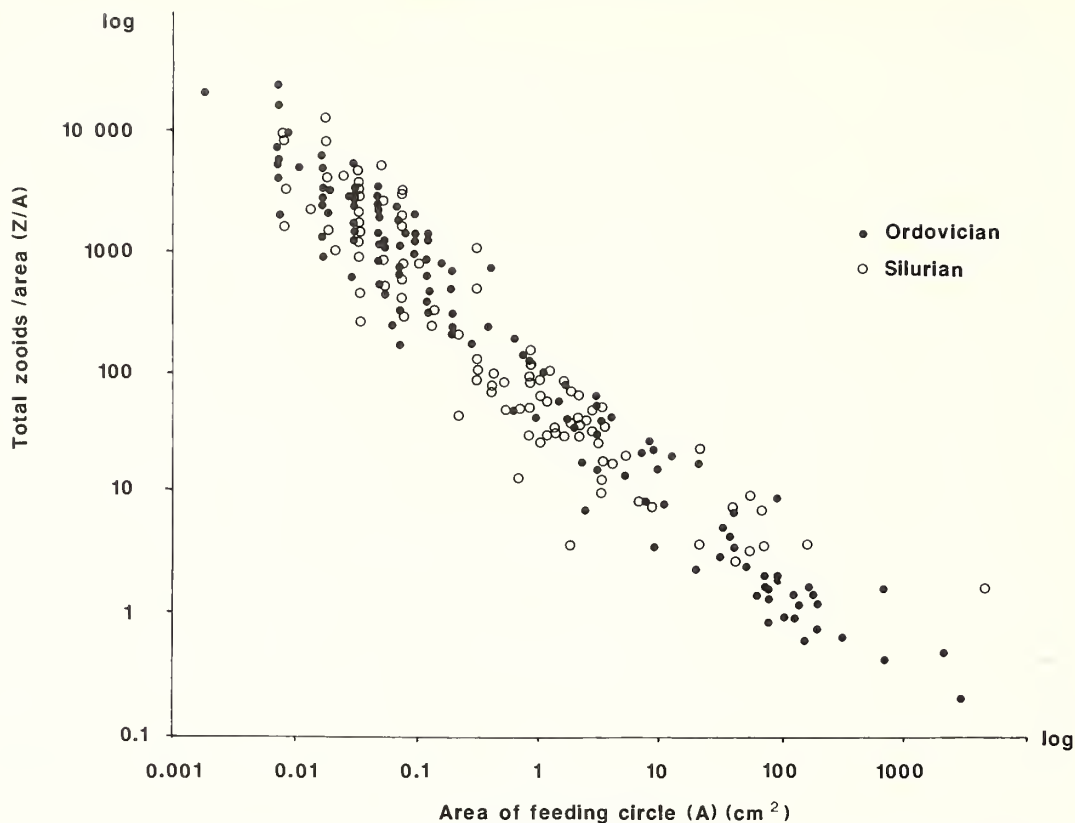
TEXT-FIG. 4. Total number of zooids in a colony plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).



TEXT-FIG. 5. Diameter of feeding circle plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom).



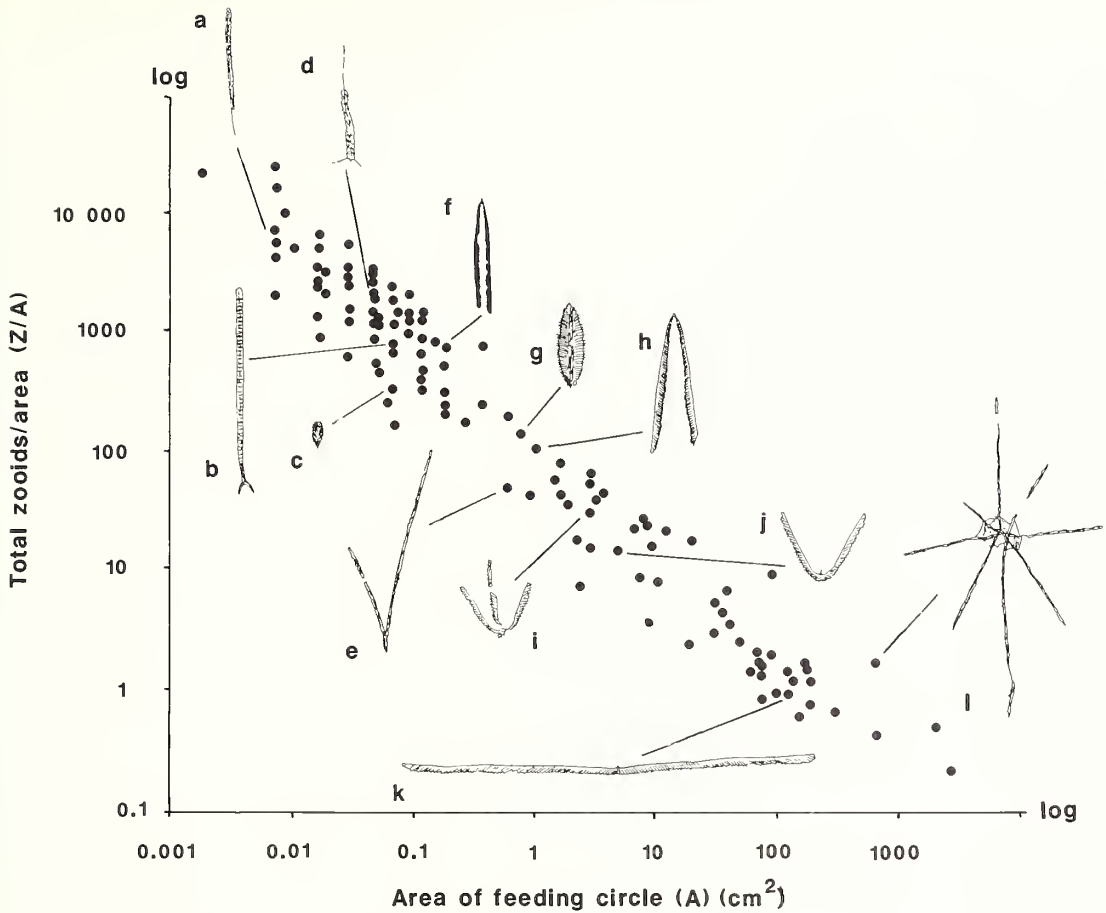
TEXT-FIG. 6. Feeding intensity, measured as total zooids/diameter of feeding circle, plotted against time (top) and summarized as a bar graph for the Ordovician and Silurian (bottom). Note that the change of scale at high feeding intensity values makes a false peak appear at the top of the bar graph. This is not a histogram.



TEXT-FIG. 7. Feeding intensity (measured as total zooids/area of feeding circle) plotted against feeding area. Note the similarity of plots for the Ordovician and Silurian data. The apparent straight line correlation is a function of using log values on both axes.

Ordovician–Silurian boundary. But this derived plot remains the same. The area of feeding circle must have changed at the same time in such a way as to result in the feeding intensity remaining the same. This is shown to have been the case in Text-figure 5 where the feeding circle of Silurian graptoloids is seen to be much smaller than that for Ordovician forms.

The shapes of rhabdosomes which produce plots in different parts of the graph are shown in Text-figure 8 for the Ordovician and Text-figure 9 for the Silurian. High intensity feeders with a small feeding circle are scandent biserial forms in the Ordovician and early Silurian. Later in the Silurian these are 'replaced' by straight monograptids. The word replaced is used in inverted commas because there is no proof that this was an active or competitive replacement within the environment. It is simply replacement in a given area of the graph, which could have been the result of passive processes unrelated to competition. However, it could indicate a refilling, in the Silurian, of feeding niches which were unoccupied following the end Ordovician extinction. The recovery after this extinction event follows the classic exponential increase in diversity after a slow initial growth in diversity. This diversity explosion probably began at the base of the *persculptus* Zone (Rickards 1988). The lowest diversity of all is found in the *extraordinarius* Zone, with only a few biserial types present. In the *persculptus* Zone these become more numerous, and rare uniserial scandent forms appear. By the top of the *acuminatus* Zone, a diverse biserial population is supplemented by dimorphograptids and several genera of scandent monograptids, including *Atavograptus*, *Lagarograptus* and *Coronograptus* (Rickards 1988).



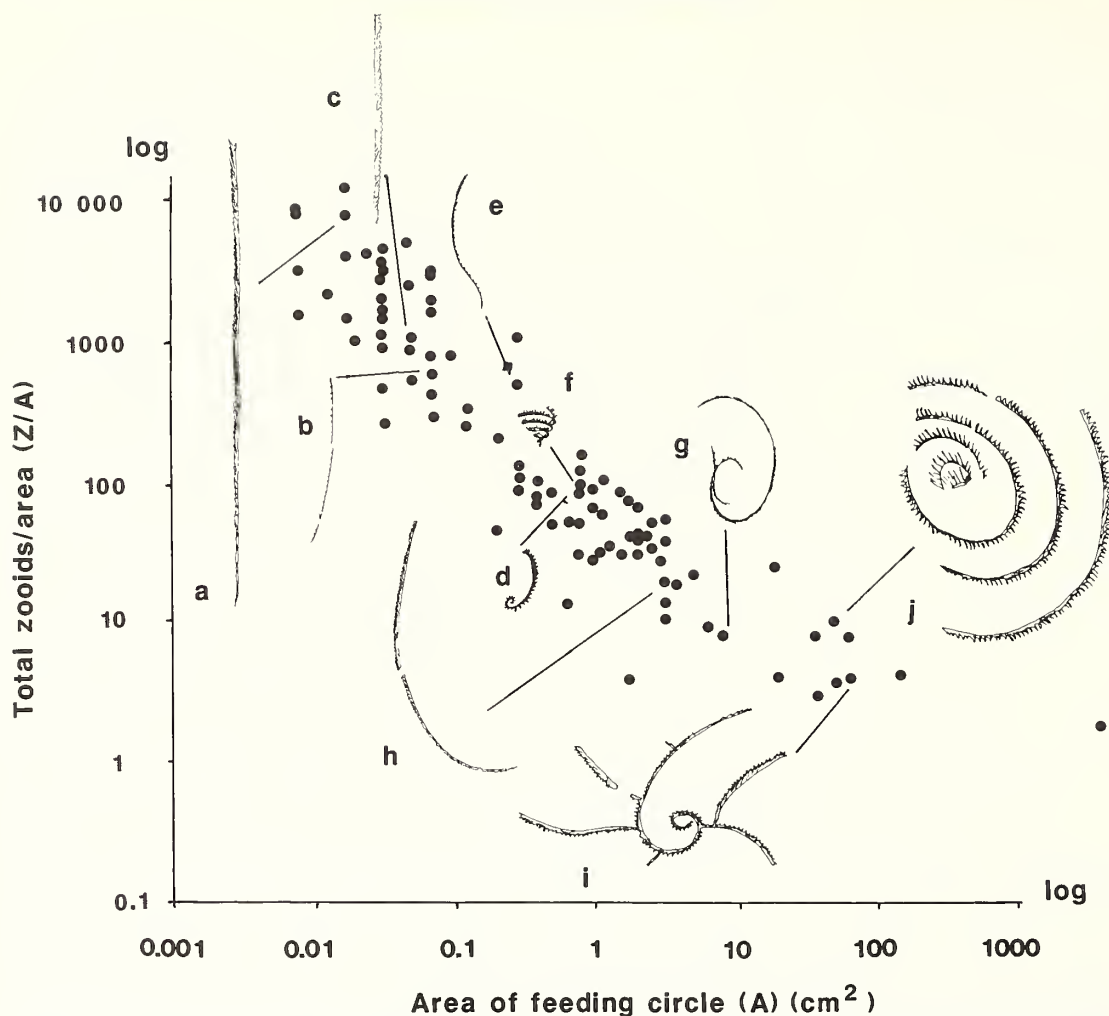
TEXT-FIG. 8. This graph demonstrates where a range of Ordovician graptoloids plot on the feeding intensity – area of feeding circle diagram. Key: a, *Amplexograptus arctus*; b, *Climacograptus bicornis*; c, *Petalograptus minor*; d, *Cryptograptus antennarius*; e, *Dicranograptus furcatus*; f, *Didymograptus stabilis*; g, *Phyllograptus cf. typus*; h, *Didymograptus bifidus*; i, *Tetragraptus reclinatus*; j, *Didymograptus gibberulus*; k, *Didymograptus hirundo*; l, *Dichograptus octobrachiatus*.

Moderate intensity feeders with moderate feeding areas are inclined biserial forms and tetragraptids in the Ordovician. In the Silurian this area of the graph is filled by curved or spiral monograptids. Large feeding area forms always have low feeding intensities. The Ordovician forms include horizontally disposed didymograptids and multiramous graptoloids like *Loganograptus*. These are 'replaced' on the Silurian graphs by cyrtograptids and other multiramous forms generated with cladia.

THEORETICAL AND STRUCTURAL LIMITS TO FEEDING STRATEGIES

Why do graptoloids plot where they do? Some theoretical limits can be applied (Text-fig. 10) because of the small number of basic morphologies adopted by graptoloids. These limits are not, in themselves, environmental indicators although the presence of a given type of graptoloid at a given locality might be.

Vertically disposed forms could not have had a very low feeding intensity unless they had very

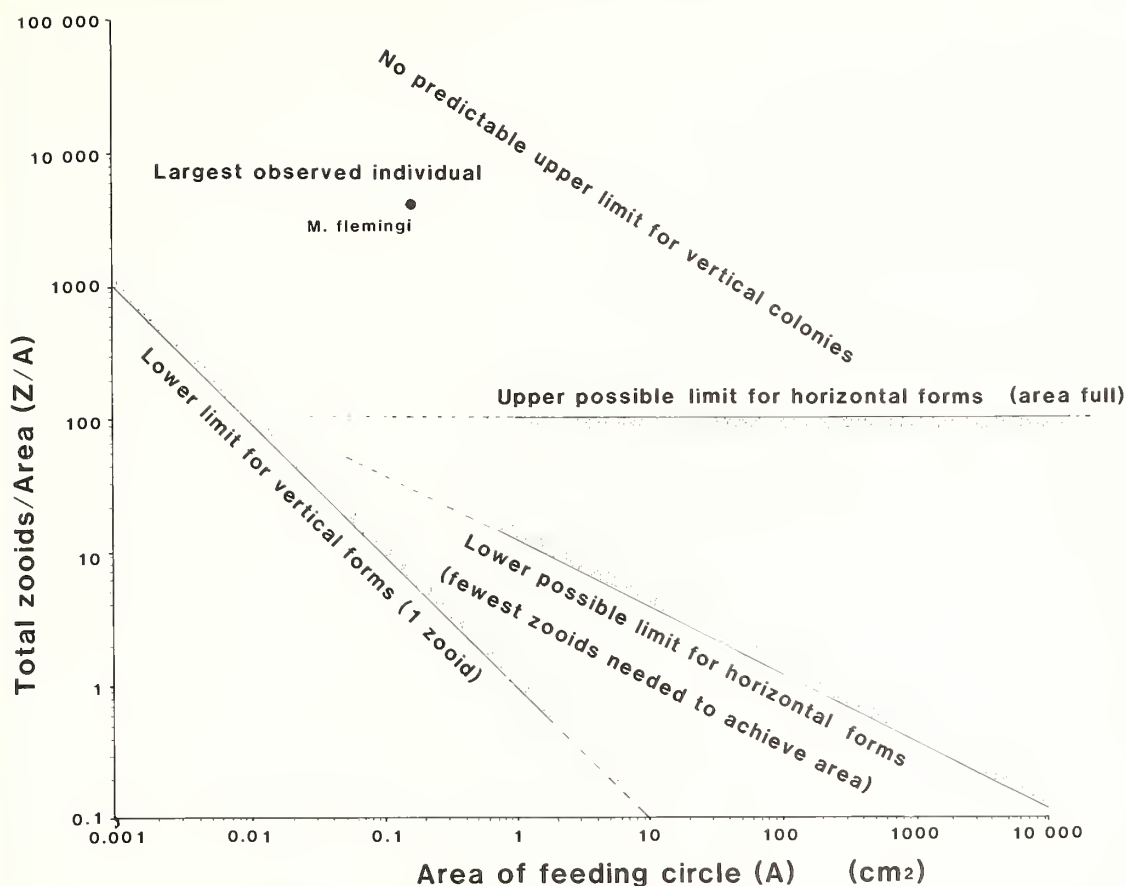


TEXT-FIG. 9. This graph demonstrates where a range of Silurian forms plot on feeding intensity – area diagrams. Key: a, *Monograptus regularis*; b, *M. barrandei*; c, *M. colonus*; d, *M. fimbriatus*; e, *M. scanicus*; f, *M. turriculatus*; g, *M. involutus*; h, *M. cyphus*; i, *Cyrtograptus murchisoni bohemicus*; j, *M. convolutus*.

broad stipes. For instance, a graptoloid with stipes 2 mm wide would need to have had less than one zooid to have a feeding intensity below 10. This is clearly impossible. A lower limit to the feeding efficiency of a vertically disposed graptoloid with any width of rhabdosome is given by the need to have had a minimum of one zooid.

No upper limit to theoretical feeding intensity can be predicted for vertically orientated forms. Some graptoloids could, perhaps, have carried on growing indefinitely, reaching higher and higher feeding intensities. The upper limits on this graph may be entirely a function of preservation – long graptoloids are less likely to be preserved intact. However, some graptoloids can be seen to have reached a mature stage where growth had ceased (C. M. Mitchell, pers. comm.), so this is not entirely the case. Long graptoloids may have become structurally weaker as they grew, or their growth may have been limited by food availability.

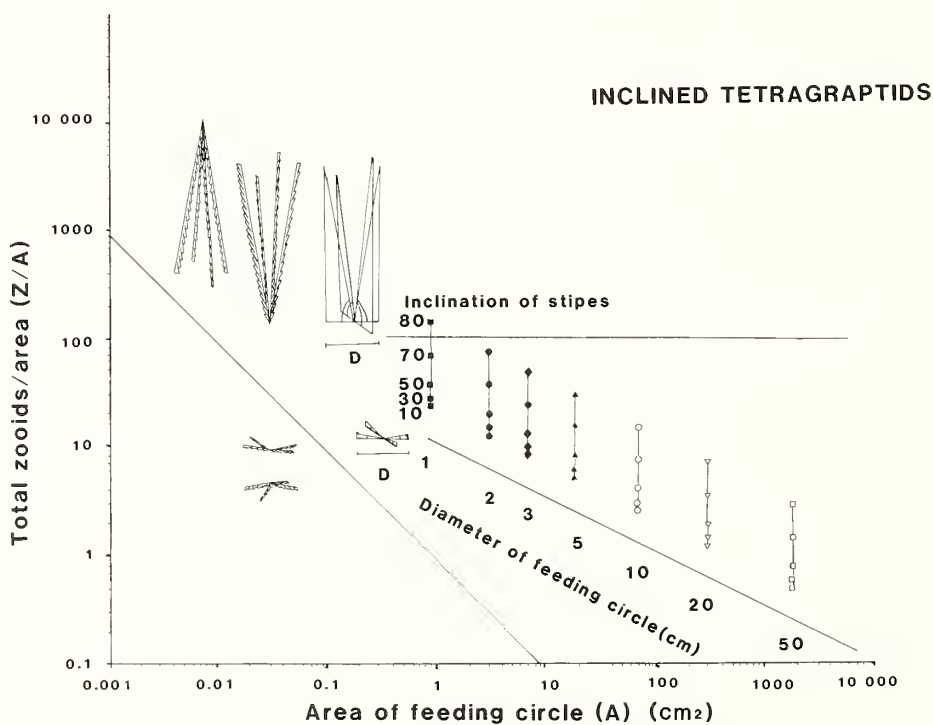
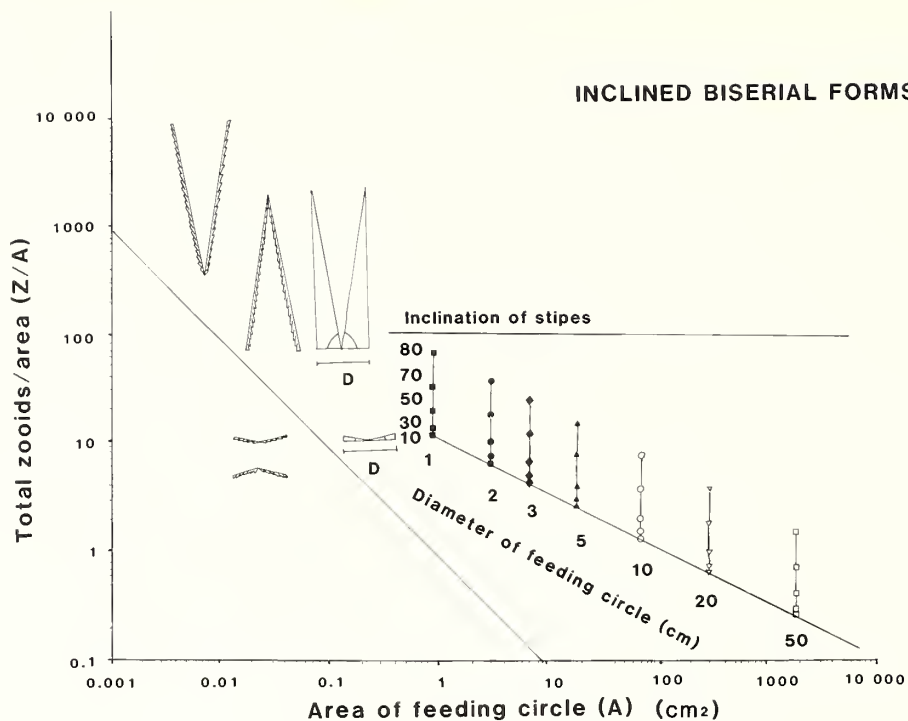
A lower possible limit for the feeding efficiency of horizontal forms is the need to cover a given diameter of feeding circle. Thus, for example, a colony with a feeding diameter of 10 cm needed at



TEXT-FIG. 10. Theoretical limits on where particular shapes of graptoloids can plot on a feeding intensity – area graph.

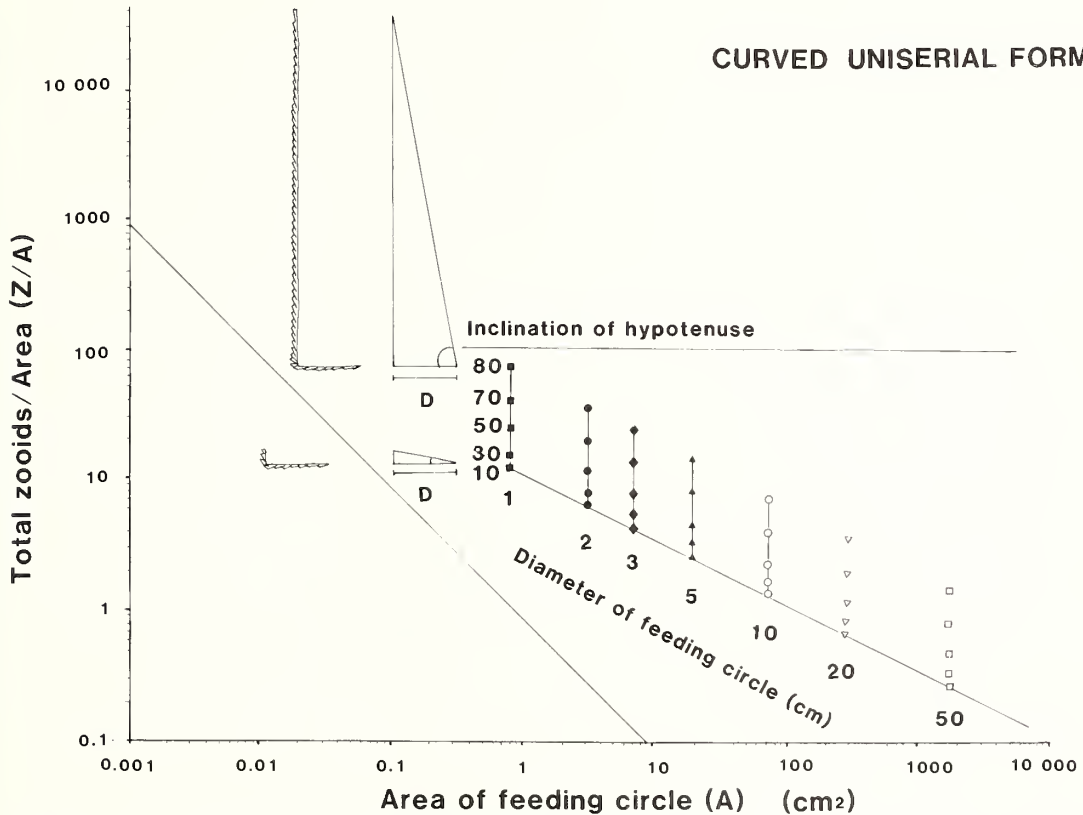
least 10 cm of stipe and would have fed over a circle of 78.5 cm^2 (πr^2 , where $r = 5$). It would inevitably have contained approaching 100 zooids, as horizontal forms tend to have around 10 zooids per cm (R. B. Rickards pers. comm.). The lowest possible feeding intensity for this form would have been $100/78.5 \text{ cm}^2$. A colony 20 cm in diameter could not have had less than about 200 zooids, and thus a feeding efficiency of $200/314.16 \text{ cm}^2$. The lowest possible feeding efficiency for horizontal forms is given by the minimum number of zooids needed to achieve a given feeding diameter.

An upper possible limit for horizontal forms can also be defined. This is where the total number of zooids filled the available space completely. In the case of a colony 10 cm in diameter, the area available for feeding on was 78.5 cm^2 . If each zooid required, for example, 1 mm^2 of space in order not to compete with its nearest neighbour, then there could have been a maximum 7850 zooids in the colony. This would have completely filled the available space. It would also have been impossible to reach because no pattern of branching arms could completely fill a circle. There is a structural upper limit imposed by the branching patterns which graptoloids evolved. However, there is good evidence to suggest that many multiramous forms developed patterns of branching which maximized their coverage of the available area (Fortey and Bell 1987). In order to increase their feeding intensity further within a given feeding circle it would have been necessary to become dome-shaped.



TEXT-FIG. 11. Inclined biserial and tetragnostid forms modelled mathematically with the region over which they plot on a feeding intensity - area graph shown.

Inclined and curved forms can be regarded as intermediate between vertically and horizontally disposed forms. For graptoloids with straight inclined stipes, lower and upper limits to feeding efficiency depended on the inclination of the stipes (Text-fig. 11). A simplifying assumption is made that the geometry of curved forms approximated to triangles with the hypotenuse missing (Text-fig. 12). This shape is rare in nature but does occur, e.g. *Monograptus limatulus*. Upper and lower limits to feeding efficiency depended on the inclination of this hypotenuse for a given areas of feeding circle.



TEXT-FIG. 12. Curved monograptids modelled mathematically with the region over which they plot on a feeding intensity – area graph shown.

The same area on the graph was covered by curved monograptids and inclined, biserial forms. Inclined tetragraptids obviously plot with higher feeding efficiencies for a given area of feeding circle.

CONCLUSIONS AND DISCUSSION

The first conclusion concerns the appearance of monograptids. The decrease in the number of stipes was matched by greater variability in the number of zooids per cm and in the width of stipe than that present in earlier forms. The degree of curvature of stipes in some species also increased.

Although the mean total number of zooids in a colony fell sharply when monograptids appeared, the mean feeding intensity, which is partly a function of total zooids, retained the same mean, mode and standard deviation across the Ordovician–Silurian boundary. This was achieved by curvature of some stipes, and by variations in the colony width for straight, scandent forms. As a result, the

log-log graphs of feeding area versus intensity are strikingly similar for the Ordovician and Silurian graptoloids. This suggests a uniformity of function beneath the obvious dissimilarity of colony forms at different times.

Changes in the number of stipes, their orientation, the total number of zooids in the colony and their packing would all have served to present the zooids of a given colony to the water an effective feeding array. Competition must have meant that forms as different as *Cyrtograptus* and *Monograptus priodon*, or *Petalograptus* and *Trochograptus* were suited to different niches. Presumably all of these forms presented effective feeding arrays, but in niches with different availabilities of food.

The feeding area – intensity plots are interpreted in the following way. High intensity feeders must have required an intense concentration of food in the environment. Conversely, a low feeding intensity is interpreted as meaning that the environment in which the graptolite lived had a low food abundance. The size of the colony can be interpreted as a measure of dependability of food supply. In order for a colony to become large, food needed to be continuously available for a relatively long period of time, unless colony growth could occur discontinuously. Small colonies may have been the result of highly variable food availability, perhaps of seasonality.

It has been suggested (Bates and Kirk 1985; R. A. Cooper, pers. comm.) that large, multiramous colonies in the lower Ordovician were confined to deep water positions. If true, it fits well into the feeding strategy model as multiramous forms were low intensity feeders. Fortey and Cocks (1986) used observations of graptoloid faunas combined with palaeogeographic reconstructions to suggest that an isograptid fauna of early Ordovician graptoloids lived in an offshore, oceanic environment. Typical genera include *Pseudisograptus*, *Oncograptus*, *Cardiograptus*, *Goniograptus* and *Signagraptus*. All of these would have had moderate to low feeding intensities.

Two general models have been proposed for graptoloid life habit. The first suggests that neutrally buoyant graptoloids remained static in the water and fed on particles of food which moved past them, at least in their early growth stages (Finney 1979). The alternative view is that graptolites were mobile in some way and moved through a column of water, either passively (Bulman 1964; Rickards 1975), or by automobility (Kirk 1967; Bates and Kirk 1985). This second view is supported by modelling experiments conducted by the author (Rigby and Rickards 1989), although the mechanism of movement remains obscure. If the first view is correct, then availability of food would have directly controlled the number of zooids per centimetre of stipe. If the second view is correct, food availability would have controlled the feeding intensity of the colony, i.e. the total number of zooids buffered by the area of water available for them to feed on.

If the mobile model is accepted, then the results of this paper should be interpreted as follows. The similarities of feeding intensity in the Ordovician and Silurian indicates the same range of productivity at both times. A reduction in the mean total zooids in the colony is compensated for by changes in stipe curvature and thickness.

If the static model of graptoloid life habit is accepted, then the results from the number of zooids per centimetre are the most important. They suggest the same average food supply across the Ordovician–Silurian boundary, but with an increased range of abundances, perhaps implying a greater range of environments. The general decrease in total zooids in a colony suggests that in general food supply was less predictable in the Silurian.

In either model, a similar level of food availability is predicted for the Ordovician and Silurian. This was exploited by graptoloids with a range of different rhabdosome shapes. Strategies for exploiting a given food abundance changed with time but can be reconstructed by means of the graphs documented here. These bring out similar patterns which have previously been hidden by the huge range of graptoloid morphology.

FUTURE WORK

It is now necessary to test this model of food availability and its control on graptoloid morphology in real locations where the palaeogeographic setting is well known. This in itself is still a major problem. Areas of upwelling should be contrasted with known high latitude sites where productivity

would also have been high but possibly more seasonal, especially when permanent ice was present at the poles. These results in turn should be compared to those from deep water sites where productivity would have been much lower but more reliable.

It is important to see how different astogenetic stages of various morphologies plot on the graphs. Horizontal colonies could theoretically have kept the same feeding intensity as they grew, but this must have changed in other forms. In curved monograptids an abrupt change must have occurred when curvature first began to develop. This is sometimes several centimetres along the stipe. There would have been a progressive increase in feeding intensity with growth in straight, scandent forms.

The biggest single problem facing this kind of investigation is that of taphonomy. Graptoloids are most often found in a broken state, where measurements of feeding areas and intensities are impossible. What is needed is a method of reconstructing graptolite assemblages from their preserved remains. Work by Budd (1990) seems to show that the rate of deposition was a primary control on graptolite break-up, with slow burial resulting in greater breakage. Computer programs allow these breakage effects to be removed. This opens the way for further study on this problem. It may eventually be possible not only to understand the ecology of graptolites much better than at present, but also to produce a useful tool for understanding the oceanography of the early Palaeozoic seas.

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MORPHOLOGY AND SHELL MICROSTRUCTURE OF CRETACEOUS THECIDEIDINE BRACHIOPODS AND THEIR BEARING ON THECIDEIDINE PHYLOGENY

by PETER G. BAKER

ABSTRACT. New morphological and microstructural information from *Bifolium faringdonense* (Davidson, 1874), *Bosquetella campichei* (de Loriol, 1872), *Thecidiopsis tetragona* (Roemer, 1839) and *Thecidiopsis bohemica imperfecta* Nekvasilová, 1967 indicates that the specimens assigned to *T. bohemica imperfecta* do not belong to *Thecidiopsis*. The organization and microstructure of the brachial valve, place *T. bohemica imperfecta* close to thecidellinids such as the Recent *Thecidellina blochmanni* Dall, 1920. In comparison with other Cretaceous monoseptate forms, differences in morphology and shell microstructure clearly separate *T. bohemica imperfecta*, *B. faringdonense* and *B. campichei*, and are considered to be distinctive enough to allow *T. bohemica imperfecta* to be assigned to a new genus, *Eothecidellina*. The discovery of canopied brachial lobes in *B. faringdonense* and rudimentary canopies in the Middle Jurassic *Moorellina dubia* (d'Orbigny, 1850), together with the clarification of the systematic position of *Eothecidellina imperfecta* (Nekvasilová), provides a much clearer picture of thecidellinid evolution. The correlation of the morphology and shell microstructure of *T. tetragona* with basal Middle Jurassic genera and the narrowing of the thecideid plexus of descent, enables a revised thecideidine phylogeny to be presented.

DISCOVERY of a Middle Jurassic thecideidine with a partially suppressed fibrous secondary shell mosaic (Baker and Elston 1984), recognition of shell microstructural features traceable over long periods of time (Baker 1989), and studies on ontogeny (Smirnova 1969, 1984) pointed to weaknesses in existing taxonomic and phylogenetic frameworks for thecideidines. The evidence indicated that conclusions about thecideidine evolution based on brachial lobe morphology (Pajaud 1970) and the time of onset of the suppression of fibrous secondary shell secretion (Williams 1973) had been premature. Smirnova's (1984) contention that *Thecidellina* arose from Upper Aptian *Bifolium* stock, prompted the restudy of Upper Cenomanian monoseptate forms previously assigned (Nekvasilová 1967) to *Thecidiopsis*, and renewal of the search (Baker and Laurie 1978) for better-preserved specimens of *Bifolium*. The further suggestion that *Thecidellina* might be traced back to a Jurassic moorellinid ancestor (Smirnova 1984) revived interest in the smaller species of *Moorellina*. When it was shown (Baker and Elston 1984; Baker 1989) that the Lower Cretaceous (Upper Valanginian) *Thecidiopsis tetragona* (Roemer, 1839) could also be traced back to Middle Jurassic (Aalenian) roots, a restudy of *T. tetragona* became necessary. Although the general *Thecidiopsis* shell succession had been established (Williams 1973; Smirnova 1979, 1984), the requirement for a clearer understanding of the detailed shell microstructure of *T. tetragona* was increased following the discovery by Baker (1989) of a parallel shell development pattern in the early Middle Jurassic *Pachymoorellina dumdriensis* (Rollier, 1915).

MATERIAL AND METHODS

Specimens of *Eothecidellina imperfecta* (Nekvasilová, 1967) from Zbyslav, Czechoslovakia, were obtained from Dr O. Nekvasilová, Academy of Sciences Prague. Specimens of *Bosquetella campichei* (de Loriol, 1872) and *Thecidiopsis tetragona* (Roemer, 1839) from Château du Marais, Auberson, were loaned from the Campiche Collection, housed in the Musée Géologique, Lausanne.

Specimens of *Bifolium faringdonense* (Davidson, 1874) were selected from material previously collected from the Faringdon Sponge Gravels (Baker and Laurie 1978) and *Moorellina dubia* (d'Orbigny, 1850) from material collected from Crickley Hill, near Cheltenham (Baker 1989).

The holotype of *Eothecidellina imperfecta* (ON-3) and paratypes ON-1, ON-2, ON-4 to ON-8 and ON-2661 to ON-2664 are housed in the Geological Institute of the Czechoslovak Academy of Sciences in Prague. The specimens of *E. imperfecta*, *Bifolium faringdonense* and *Moorellina dubia* figured in this paper (BD9023–BD9028) are housed in the British Museum (Natural History). The specimens of *Bosquetella campichei* (reg. no. 42530) and *Thecidiopsis tetragona* (reg. nos 42531–42533) are housed in the Musée Géologique, Lausanne.

The techniques used for the recovery and preparation of *E. imperfecta* were fully documented by Nekvasilová (1967, p. 117) and require no elaboration here. Similarly, for the recovery and preparation of *B. faringdonense* specimens see Baker and Laurie (1978, p. 557), and for *M. dubia* see Baker and Elston (1984, p. 777).

SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883
 Suborder THECIDEIDINA Elliott, 1958
 Superfamily THECIDEACEA Gray, 1840
 Family THECIDEINIDAE Elliott, 1958
 Subfamily THECIDEININAE Elliott, 1953
 Genus EOTHECIDEININA gen. nov.

Etymology. From the Greek *eos* (dawn) after the very early appearance of canopied intrabrachial cavities of the thecidellinid type.

Type species. *Thecidiopsis (Thecidiopsis) bohémica imperfecta* Nekvasilová, 1967.

Age. Upper Cretaceous, Upper Cenomanian.

Diagnosis. Small endopunctate thecidellinin, pedicle valve typically with a flat, well defined ventral interarea, shallow anterior sulcus and relatively large, rounded-triangular attachment scar, brachial valve with intrabrachial cavities roofed by perforate canopies and a long, straight, median septum onto which the characteristic pustulose ornament of the subperipheral rim is extended.

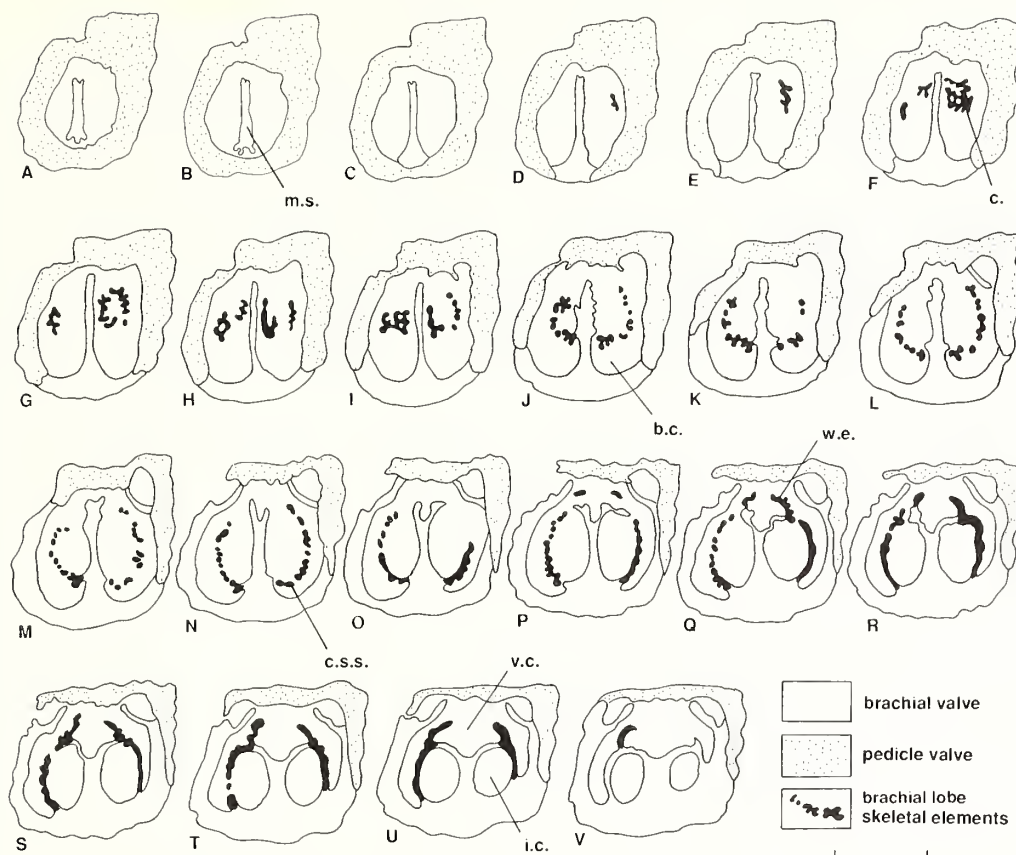
Eothecidellina imperfecta (Nekvasilová, 1967)

Plate 1, figs 1–6; Plate 3, figs 1–3; Plate 4, figs 1–7;
 Text-figs 1, 4A–C, 5A–C, 6C

- 1868 *Thecidium* sp.; Schloenbach, p. 156, pl. 5, fig. 9
- 1959 *Thecidiopsis (Thecidiopsis) bohémica* Backhaus; Nekvasilová, p. 147; pl. 11, figs 1–4.
- 1967 *Thecidiopsis (Thecidiopsis) bohémica imperfecta* Nekvasilová, p. 115–136, pls 1–8; text-figs 1–11.
- 1968 *Thecidiopsis bohémica imperfecta* Nekvasilová; Pajaud, p. 45.
- 1968 *Thecidiopsis bohémica imperfecta* Nekvasilová; Smirnova and Pajaud, p. 143.
- 1970 *Thecidiopsis bohémica imperfecta* Nekv.; Pajaud p. 208, pl. 4, fig. 2.
- 1972 *Thecidiopsis (Thecidiopsis) bohémica* Backhaus; Smirnova, p. 123.

Type specimens. Holotype ON-3, paratypes ON-1, ON-2, ON-4 to ON-8, ON-2661 to ON-2664, hypotypes BD9023–BD9025.

Distribution. The locality from which the type material was obtained is given as Zbyslav, near Čáslav, Bohemia, Czechoslovakia. The species has, however, been recorded from a number of other Bohemian localities, namely



TEXT-FIG. 1. *Eotheidellina imperfecta* (Nekvasilová). A–V, 'Wild' stereomicroscope traces of cellulose acetate peels (8–25, out of series 1–49) of serial sections through the median septum and brachial lobes of specimen BD 9024. Plane of section horizontal, relative to the surface of the brachial lobes; intersecting the commissural plane with an angle of about 5° ventral deflection. Abbreviations: b.c., brachial cavity; c., brachial lobe canopy; c.s.s. canopy skeletal support; i.c., intrabrachial cavity; m.s., median septum; v.c., visceral cavity; w.e., wing-like extension. Peel interval approximately 20 μ m. Scale bar represents 1.0 mm.

Kamajka and Starkoč near Čáslav, Kank near Kutná Hora, Vitězov near Velim, Skalka near Zehušice and Předboj near Prague. At all the recorded localities the material was collected from sediments of Upper Cenomanian age, approximating stratigraphically to a *plenus* Zone position.

Diagnosis. *Eotheidellina* up to about 2.5 mm in length, 1.9 mm wide and 2.00 mm thick. Outline roughly pyriform; dorsiconvex initially, but developing a characteristically triangular lateral profile after the appearance of the free ventral wall. Pseudodeltidium flat, parallel with the surface of the ventral interarea, demarcated only by indistinct grooves. Hinge line straight with a ratio of length to shell width of approximately 0.5. Brachial valve moderately convex with a small hypercline dorsal interarea.

Description. Small, roughly pyriform thecidellinid, with a relatively large attachment scar and well developed free ventral wall giving rise to a characteristically triangular lateral profile. The ventral interarea is clearly developed with a flat indistinct pseudodeltidium. The moderately convex brachial valve has a small but well defined hypercline dorsal interarea.

MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE OF
EOTHECIDELLINA IMPERFECTA

Valve characters

Pedicle valve. Hemispondylium raised, with clearly defined dental ridges, hemispondylial plate and supporting septum, rising from a weakly developed median ridge. The teeth are clearly cyrtomatodont and not widely separated. The inner surface of the valve is ornamented by scattered tubercles. In the anterior sector the tubercles are arranged in more linear series and many coalesce to form low ridges on the inner surface of the free ventral wall.

Brachial valve. (Pl. 1, figs 3–6; Text-figs 1, 4b, 5A–C, 6c). The cardinal margin is straight, extending for slightly more than half the maximum width of the valve. The cardinal process is relatively large, faintly trilobed, and with a characteristic dorsal deflection. The sides diverge anteriorly to form well developed inner socket ridges. The lateral adductor muscle scars are erect (orientated almost perpendicular to the commissural plane) and asymmetrically pyriform as a result of constriction by the cardinal process. The brachial bridge is well developed. The outer surface of the subperipheral rim is ornamented by up to four rows of small tubercles, with the tubercles of each row usually offset by one half phase relative to adjacent rows. The inner margin of the subperipheral rim is characterized by a row of elongate impressed areas which have been identified by Williams (1973, p. 48, fig. 10) as lophophore muscle scars. The tuberculate ornament of the subperipheral rim extends onto the median septum which is typically long and prominent, relatively thick anteriorly and, posteriorly, arching over the visceral cavity. The brachial cavities are occupied by medium-sized brachial lobes which are developed as perforate canopies over intrabrachial cavities. The brachial lobes are invariably broken in separated valves, so that the intrabrachial cavities are exposed as two shallow, roughly oval depressions, characteristically ringed by the damaged canopy skeletal supports (Pl. 1 fig. 3; Pl. 3, fig. 3). Each complete brachial lobe, therefore, represents a sort of posteriorly open, perforate calcareous sac (Text-fig. 6c), situated on either side of the median septum and slightly contiguous with it posteriorly. A previously unrecorded feature of the brachial lobes is the development of a pair of wing-like extensions (Text-fig. 1r) arching backwards into the visceral cavity. The broken remains of these structures can be identified (Pl. 1, figs 4 and 5), even in brachial valves in which the brachial lobes have been substantially damaged.

Ontogeny

The early ontogeny of *E. imperfecta* is not known. All the characters of pedicle and brachial valves are present in the smallest valves available. In the pedicle valve, the beginning of the development of the free ventral wall is thought to coincide with the onset of sexual maturity (Nekvasilová 1967,

EXPLANATION OF PLATE I

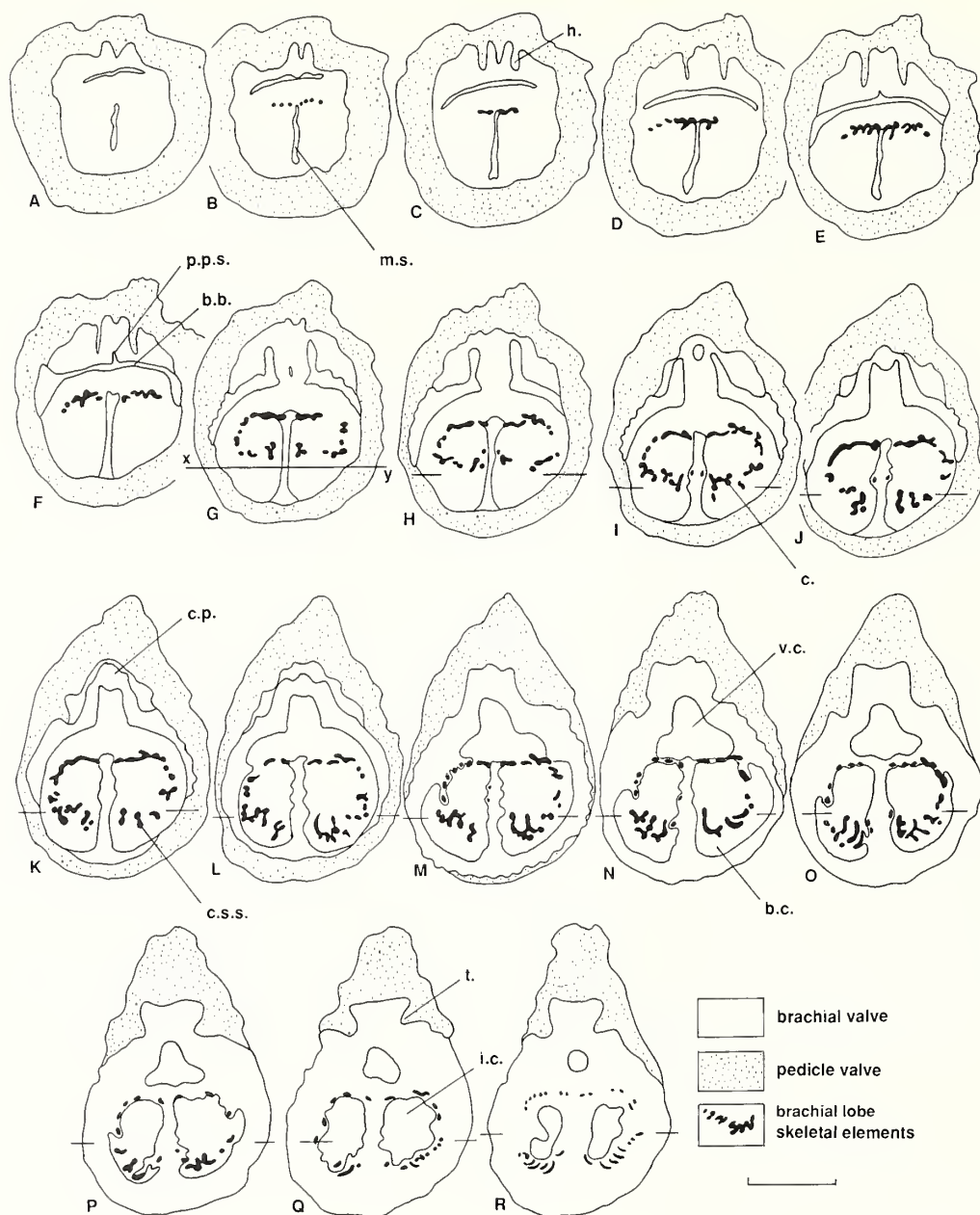
Figs 1–6. *Eothecidellina imperfecta* (Nekvasilová). Upper Cenomanian of Zbyslav, Czechoslovakia. 1 and 2, BD 9023; brachial and three-quarters profile views, photographic record, of hypotype sectioned complete shell, $\times 18$. 3–6, BD 9025; brachial anterior, three-quarters profile and posterior views of a hypotype to show the morphology typical of separated brachial valves in which the brachial canopies have been destroyed, exposing the intrabrachial cavities, $\times 20$.

Figs 7–11. *Bifolium faringdonense* (Davidson). Upper Aptian; Faringdon, Oxfordshire. 7–10, BD 9026; brachial, posterior, lateral and anterior views, photographic record, of hypotype sectioned complete shell, $\times 20$. 11, BD 9027; interior of hypotype brachial valve showing the remains of brachial canopies and the intrabrachial cavities filled with quartz grain matrix, $\times 18$.

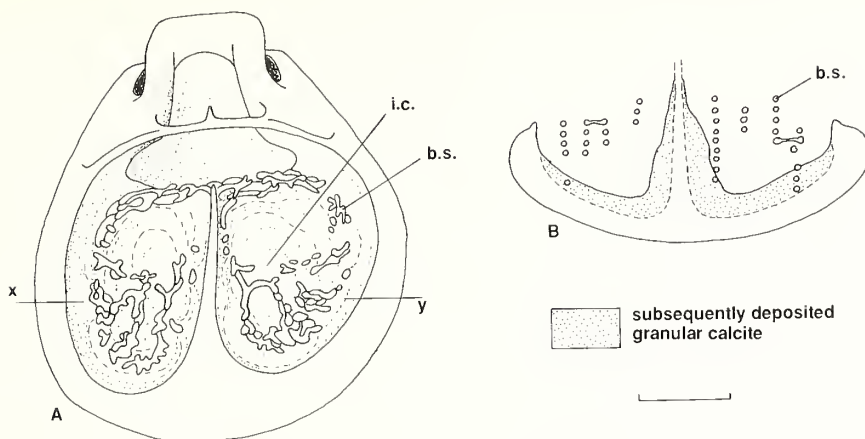
Figs 12–14. *Bosquetella campichei* (de Loriol). Upper Valanginian; Auberson; Musée Géologique, Lausanne, 42530; posterior, three-quarters profile and brachial views, photographic record, of hypotype sectioned brachial valve, $\times 12$.

All scanning electron micrographs of gold-coated material.





TEXT-FIG. 2. *Bifolium faringdonense* (Davidson). A-R, 'Wild' stereomicroscope traces of cellulose acetate peels (13-30, out of series 1-36) of serial sections through the median septum and brachial lobes of specimen BD 9026. Plane of section horizontal, approximately parallel with the commissural plane. Abbreviations as in Text-figure 1, plus: b.b., brachial bridge; c.p., cardinal process; h., hemispondylium of pedicle valve; p.p.s., posteriorly projecting spur; t., hinge tooth. Peel interval approximately 25 μ m. Scale bar represents 1.0 mm.



TEXT-FIG. 3. *Bifolium faringdonense* (Davidson). Partial reconstruction of the brachial lobes of serially sectioned specimen BD 9026, with no attempt to hypothesise the nature of the connection of the skeletal elements between successive peels. A, brachial view. B, vertical plot of peel data along x-y (Text-figs 2 and 3A) for acetate peels 19–33 (Text-fig. 2G–R inclusive), to show the brachial lobe skeletal elements in tranverse location, forming a canopy over the intrabrachial cavities. Abbreviations; b.s., brachial lobe skeletal elements; i.c., intrabrachial cavity. For ease of correlation of peel traces with original acetate peels, left is plotted as viewed, not anatomically. Scale bar represents 0.5 mm.

p. 125). In the brachial valve, ontogenetic development is characterized by slight changes in the relative proportion of the median septum and the brachial lobes, and also by increasing dorsal deflection of the cardinal process. The median septum, initially quite stubby, becomes increasingly blade-like. The immature brachial lobe canopies are characterized by relatively large, more irregular perforations which are reported to be gradually sealed as the brachial lobes mature (Nekvasilová 1967, p. 126).

Microstructure (Text-fig. 4A–C)

Although the shell shows the suppression of fibrous secondary shell typical of Cretaceous thecideidines, *E. imperfecta* is unusual among Upper Cretaceous species in that fibrous secondary shell remains a major component of the pedicle valve.

Pedicle valve. A thick granular primary layer is present, underlain by fibrous secondary shell. The fibrous secondary shell layer appears to be partially suppressed and is absent from the attachment scar area. It is, however, present as a continuous thin sheet over the entire area of the free ventral wall (Text-fig. 4C). In this region the granular calcite layer is approximately 75 μm thick, almost half the thickness of the shell wall. Sections (Pl. 4, figs 1–5) show that, at its inner boundary, the granular layer is longitudinally invaginated into the fibrous layer and eventually may become pinched off to form flattened tubercle cores surrounded by fibrous secondary shell. The development pattern seems to restrict the formation of tubercles to a single row in antero-lateral sectors of the valve. However, the thickened median ridge (Pl. 4, fig. 7) can clearly be seen to have originated from a succession of such structures, sandwiched between sheets of fibrous secondary shell. A normal orthodoxy stacked fibrous secondary shell succession (Williams 1973) is also seen in the hinge teeth.

Brachial valve. The secretion of fibrous secondary shell is almost completely suppressed, secondary fibres only occurring on the sides of the cardinal process and the inner socket ridges (Pl. 3, fig. 2). The remainder of the shell (Text-fig. 4B) is composed of granular calcite (Pl. 3, fig. 1; Pl. 4, fig. 6) in which the mainly equant granules are up to 3.0 μm in diameter.

MORPHOLOGY AND SHELL MICROSTRUCTURE OF OTHER CRETACEOUS THECIDEIDINES

Bifolium faringdonense (Davidson), Upper Aptian

Morphology. The morphology of *B. faringdonense* has been described by Elliott (1948) and Pajaud (1970) with additional comments by Baker and Laurie (1978). The form of the brachial lobes has always been interpreted from their morphology as seen in separated brachial valves. The inadequacy of this approach was noted by Nekvasilová (1967), but the weakly coherent matrix of complete shells frustrated attempts (Baker and Laurie 1978, p. 557) to obtain reliable evidence from Faringdon specimens.

Recently, however, a brachial valve with partially preserved brachial lobes was discovered (Pl. 1, fig. 11; Pl. 2, fig. 6), and also a complete shell (Pl. 1, figs 7–10) filled with crystalline calcite. The latter when serially sectioned (Text-fig. 2) enabled the first full description of the brachial apparatus of *B. faringdonense*. The previously described auriform structures (Pajaud 1970, p. 193; Baker and Laurie 1978, p. 563) are identified as the damaged supports of a network of skeletal strands almost 40 µm thick, anastomosing to form perforate canopies, partially roofing the intrabrachial cavities (Text-figs 3 and 6B). The posteriorly projecting spur, first observed in juveniles (Baker and Laurie 1978, p. 568) is confirmed by the current study (Text-figs 2F and 3A).

Microstructure. Previous studies of shell microstructure (Williams 1973, p. 465; Baker and Laurie 1978, p. 569) have shown that, with the exception of the teeth and inner socket ridges, fibrous secondary shell is replaced by granular calcite in *B. faringdonense*. Splayed acicular crystallites are associated with the development of tubercles in the subperipheral rim. The current study reveals the presence of secondary fibres in the sides of the cardinal process. Also, in (presumably aged) adults the brachial valve is so thickened by the subsequent deposition of granular calcite, that the skeletal supports of the brachial lobe canopies become substantially buried (Text-figs 2Q, R and 3B).

Bosquetella campichei (de Loria), Upper Valanginian (Pl. 1, figs 12–14)

Microstructure

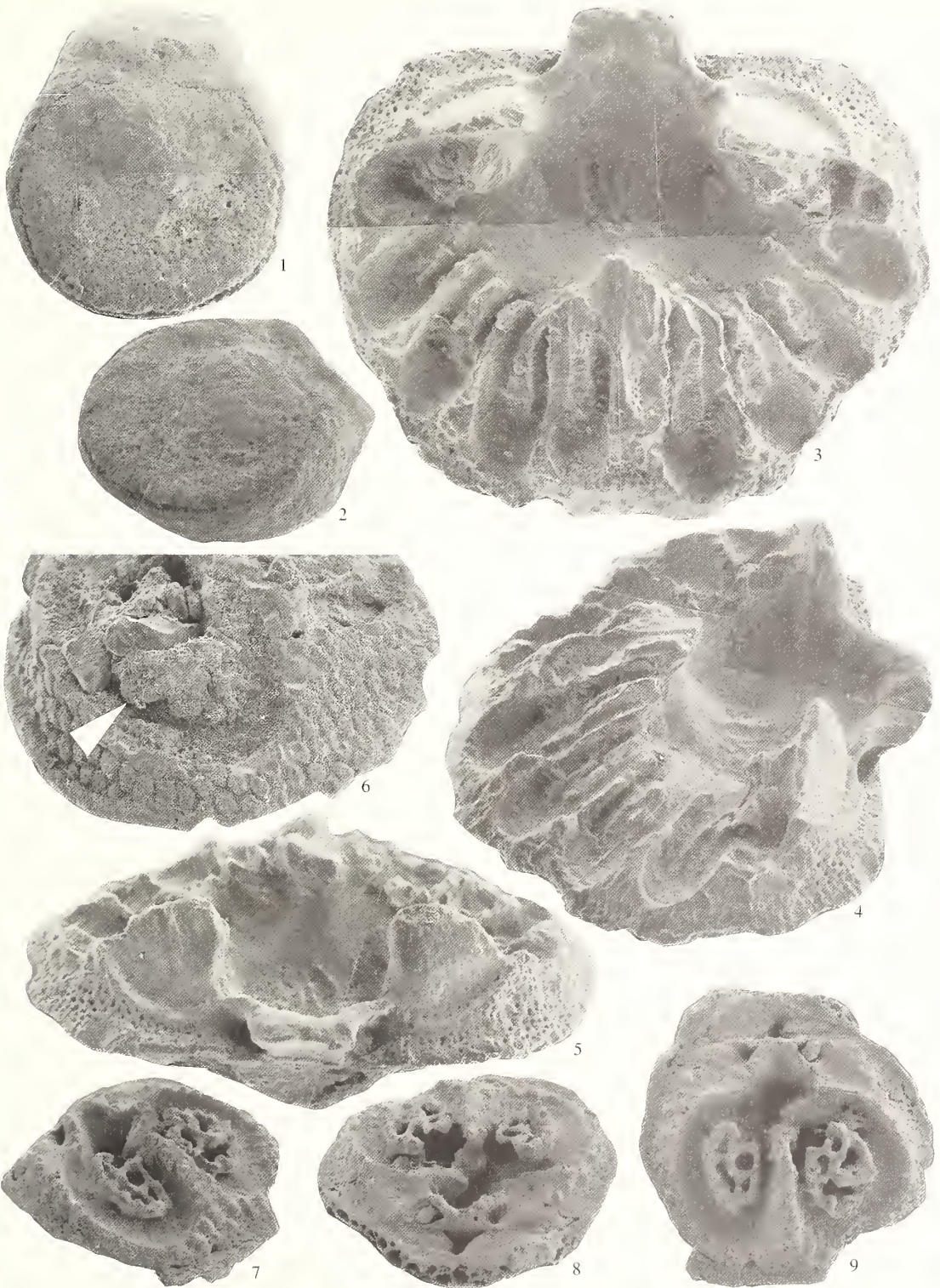
Pedicle valve. No pedicle valve was available for study from the Campiche Collection, but Smirnova (1984) described pedicle valves from Solovevka, Crimea, in which tubercle cores of granular calcite are pinched off from the primary layer and enveloped by secondary fibres in a manner very similar to that seen in *E. imperfecta*. In *B. campichei*, however, unlike *E. imperfecta*, fibrous shell is underlain by granular calcite (Smirnova 1984, pl. 23, fig. 1).

Brachial valve. Fibrous secondary shell is strongly suppressed so that, with the exception of the

EXPLANATION OF PLATE 2

Figs 1–5. *Thecidiopsis tetragona* (Roemer). Upper Valanginian; Auberson; Musée Géologique, Lausanne. 1 and 2, 42531; brachial and three-quarters profile view, photographic record, of a sectioned young adult complete shell, × 12. 3–5, 42532; brachial, tilted lateral and posterior views showing the morphology typical of separated brachial valves and the interdigitation of brachial lobes (all damaged) and lateral septa, × 15. Fig. 6. *Bifolium faringdonense* (Davidson). Angled view (rotation, 45°; tilt angle, 50°) of the right brachial cavity of specimen BD 9027, showing the remains of the brachial canopy (arrowed) in more detail, × 30. Figs 7–9. *Moorellina dubia* (d'Orbigny). Aalenian; Crickley Hill, near Cheltenham; BD 9028; three-quarters profile, posterior and brachial views of a hypotype showing the almost intact brachial lobes in the form of rudimentary canopies; the external surface of this specimen (especially figure 8, lower) is encrusted by a bryozoan, × 30.

All scanning electron micrographs of gold-coated material.



cardinal process and inner socket ridges, the brachial valve consists of a single layer of microcrystalline calcite. This consists of equant grains about $3.5\ \mu\text{m}$ in diameter (Pl. 3, fig. 7) but, in the subperipheral rim and areas close to it where resorption has occurred, tubercle cores are formed from acicular crystallites which show the same splayed orientation (Pl. 4, fig. 8) as that found in *Bifolium faringdonense*.

Thecidiopsis tetragona (Roemer), *Upper Valanginian* (Pl. 2, figs 1–5)

Microstructure

Smirnova's (1979, 1984) studies revealed that in *T. tetragona* fibrous secondary shell is strongly suppressed. She identified a primary layer of granular or acicular calcite underlain principally by granular calcite, with or without the presence of fibrous secondary shell. Secondary fibres are restricted to the hinge teeth and the hemispondylium, and to occurrence as irregular bundles in the wall of the pedicle valve. In the brachial valve, secondary fibres are only to be found in the inner socket ridges. Additionally in *T. tetragona*, the secondary shell mosaic was reported (Smirnova 1979, p. 340) to be complicated by the inclusion of 'rod-like' bodies and 'fir-tree' structures.

Pedicle valve. (Text-fig. 4F). Detailed investigation of serially sectioned specimens from the Campiche Collection, confirms the presence of a thin granular primary layer and enables the so-called, rod-like bodies, to be identified as acicular crystallite tubercle cores (Baker 1989, p. 62) of the type found in *Pachymoorellina*. Sections parallel with the boundary of the primary layer show that the tubercle cores are initiated through 'seeding' acicular crystallites on to its inner surface (Pl. 5, fig. 1). Initially, the tubercle cores remain separated by granular calcite (Pl. 5, fig. 2) but as they develop, this is gradually excluded and the tubercle cores come into lateral contact with their neighbours (Pl. 5, fig. 7). Each generation is usually offset by a half-phase so that, in oblique section, a very characteristic overlapping 'fish-scale' effect is produced (Pl. 5, fig. 8). In high oblique or transverse section (Pl. 5, fig. 4) the tubercle cores often appear to have a centre column of granular calcite. This is usually a consequence of the splayed arrangement of acicular crystallites forming the tubercle core. Crystallites in near axial orientation will be sectioned transversely (Pl. 5, fig. 3) and give the appearance of being granular. Some tubercle cores, however, do appear to have an axial structure in which scalenohedra-like bodies (Pl. 5, fig. 5) are mixed with the axially orientated acicular crystallites. Away from the hinge teeth and hemispondylium, where it is well represented, fibrous secondary shell is restricted to the inner margin of the free ventral wall. It occurs as irregular, attenuated strands (Pl. 5, figs 3 and 6), pinched and deflected by the development of the acicular

EXPLANATION OF PLATE 3

Figs 1–3. *Eothecidellina imperfecta* (Nekvasilová). All BD 9025. 1, granular calcite shell and endopuncta (top left) in the floor of the left brachial cavity, $\times 2000$. 2, right inner socket ridge (socket, lower centre) showing the development of fibrous secondary shell, $\times 150$. 3, left brachial cavity showing detail of the broken canopy supports, ringing the intrabrachial cavity (upper right), $\times 100$.

Figs 4 and 5. *Thecidiopsis tetragona* (Roemer). 4, 42531; granular primary layer, $\times 4000$. 5, 42532; coarser secondarily deposited granular calcite (cf. Fig. 4) in the floor of the brachial cavity, associated with the development of the brachial lobes, $\times 2000$.

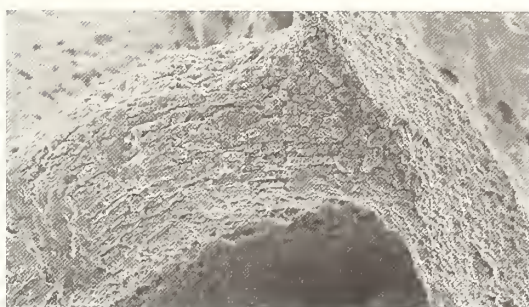
Figs 6 and 7. *Bosquetella campichei* (de Loriol). 6, 42530; enlarged view of the brachial cavities showing the asymmetrically pyriform brachial lobes and absence of intrabrachial cavities, $\times 35$. 7, fracture surface on the median septum of the same specimen; showing the granular calcite shell, $\times 3000$.

Figs 8 and 9. *Moorellina dubia* (D'Orbigny). 8, BD 9028; enlarged view of the right brachial cavity showing detail of the canopy and the nature of the canopy skeletal supports, $\times 130$. 9, same specimen; showing the typical partially resorbed moorellinid fibrous secondary shell, $\times 3000$.

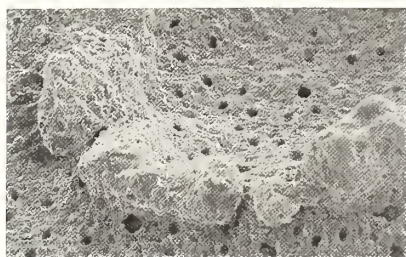
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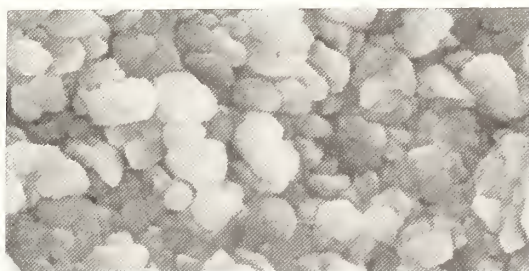
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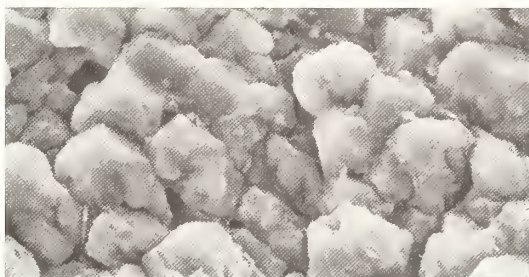
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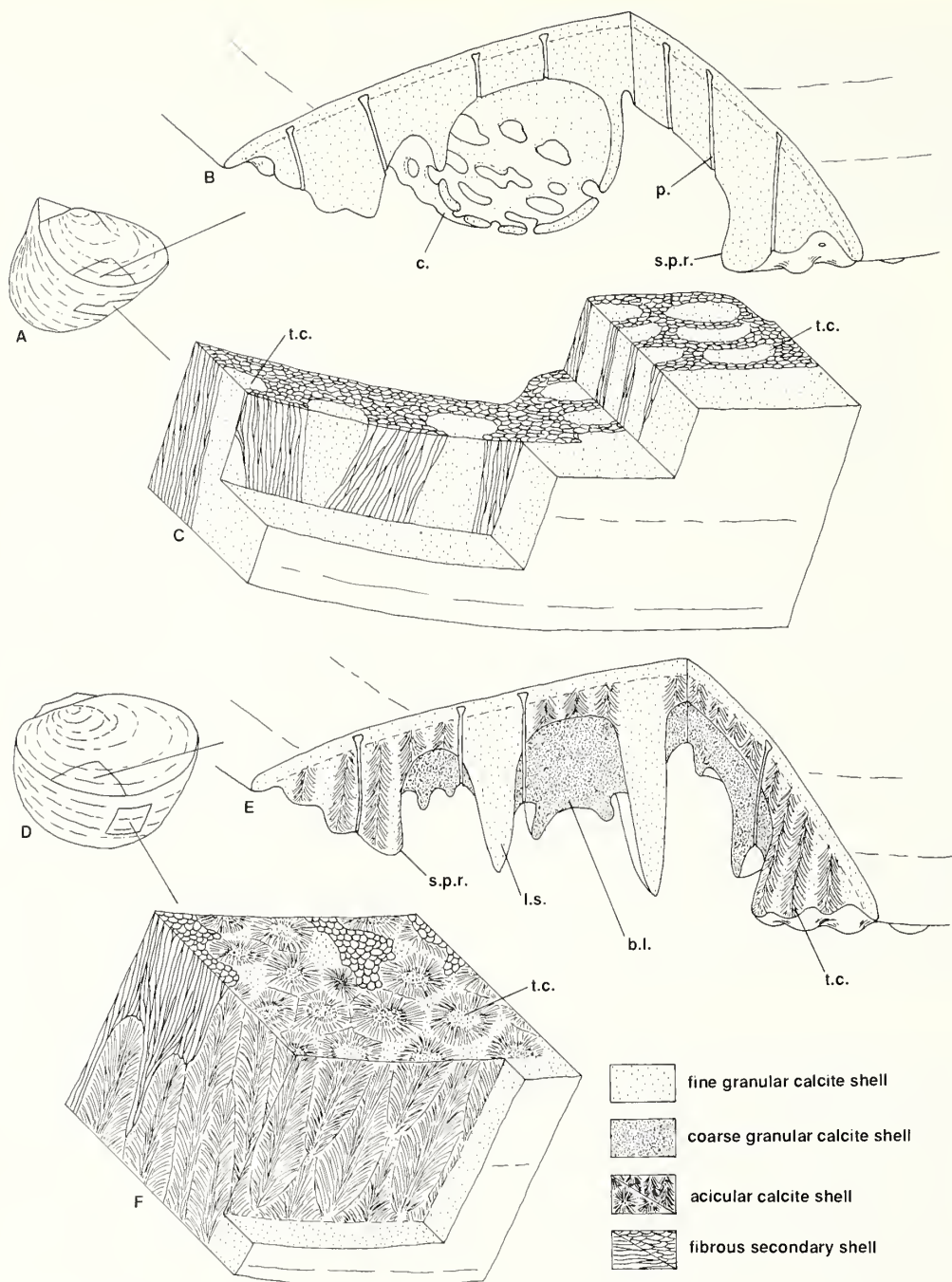
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TEXT-FIG. 4. Diagrammatic reconstruction of the shell microstructure of A–C, *Eothecidellina imperfecta* (Nekvasilová) and D–F, *Thecidiopsis tetragona* (Roemer). A, D, locational diagrams. B, E, block diagrams showing the microstructure of brachial valves. C, F, block diagrams showing the microstructure of pedicle valves. Abbreviations: b.l., brachial lobe interdigitation; c., brachial lobe canopy; l.s., lateral septum; p., endopuncta; s.p.r., subperipheral rim; t.c., tubercle core.

crystallite tubercle cores. In view of their abrupt appearance close the inner surface of the shell wall, these groups of secondary fibres must, presumably, originate from epithelial cells which had previously been secreting acicular calcite. Somehow the 'memory' of certain cells is triggered and fibrous secondary shell is secreted.

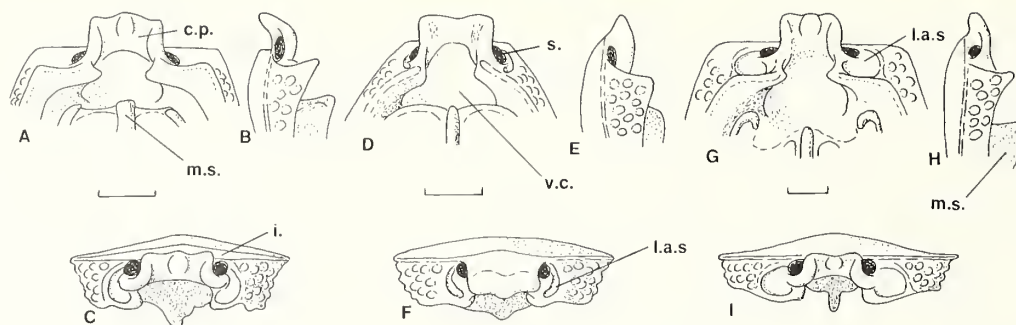
Brachial valve. (Text-fig 4E). Smirnova (1979, p. 340) described the brachial valve as double layered, with an outer crystalline layer containing 'fir-tree' structures, aligned nearly perpendicular to the external surface of the valve. The fir-trees were reported to be abruptly cut off from the granular calcite inner layer. Serially sectioned Campiche specimens show that the fir-trees (subsequently called 'herring-bone' patterns by Smirnova (1984)) are the equivalent of the acicular crystallite splays (Baker and Laurie 1978, p. 564, text-fig. 5D) found in the tubercle cores of *Bifolium*. In *T. tetragona* the wall of the brachial valve is thickened as a result of the increasing development of the brachial lobes and their interdigitation with the lateral septa. The inner layer described by Smirnova is the product of deposition of granular calcite in areas where shell resorptive activity had previously been operative. The cut-off, therefore, as in *Pachymoorellina dundriensis* is really the trace of the transgression across an older resorption surface. As in *P. dundriensis* the secondarily deposited granular calcite is coarser (Pl. 3, fig. 5) than the granular calcite underlying the transgression surface (Pl. 3, fig. 4). Clearly, the so-called third layer (Smirnova 1979, p. 340) associated with the development of the hemispondylium in the pedicle valve of *T. tetragona* has the same origin. Similar transgression surfaces have been identified in *Thecidellina barretti* (Davidson, 1864) by Williams (1973, p. 452, fig. 26).

DISCUSSION

Eothecidellina imperfecta may be distinguished from *Bifolium faringdonense* and *Bosquetella campichei* through differences in morphology and shell microstructure. Brachial, posterior and lateral views of the dorsal cardinalia (Text-fig. 5) show that the lateral adductor muscle scars differ in shape, orientation and disposition. In *E. imperfecta* the cardinal margin is straight and slightly more than one-half the width of the valve (Text-fig. 5A), whereas in *B. faringdonense* it is very short, usually not extending beyond the boundary of the dental sockets (Text-fig. 5D). *B. campichei* also has a straight cardinal margin but the cardinal process is relatively, much smaller (Text fig. 5G) than that of *E. imperfecta*. The cardinal process differs in attitude (Text-fig. 5B, E, H). *E. imperfecta* has a small hypercline dorsal interarea (Text-fig. 5C), a feature not seen in *B. faringdonense* or *B. campichei* (Text-fig. 5F, I). The configuration of the brachial lobes as indicated by their skeletal elements is oval in *E. imperfecta* and *B. faringdonense* (Pl. 1, figs 3 and 11) and the canopies overarching the intrabrachial cavities are more completely developed in *E. imperfecta* than in *B. faringdonense*. In *B. campichei* the brachial lobes are asymmetrically pyriform (Pl. 1, fig. 14). There are no intrabrachial cavities (Pl. 3, fig. 6) and, as far as is known, the skeletal elements of the brachial lobes are not overarching.

With the exception of the inner socket ridges and sides of the cardinal process, the brachial valve of *E. imperfecta* appears to be composed entirely of granular calcite. There is no differentiation into acicular crystallites as seen in *B. faringdonense* and *B. campichei*. In the pedicle valve, the tubercle cores clearly originate in the same way in *E. imperfecta* and *B. campichei*, but in *B. campichei*, the tubercle cores are not stacked to form a median ridge. In *E. imperfecta* fibrous secondary shell forms a complete inner lining, whereas, in *B. campichei* the inner shell layer is composed of granular calcite. No tubercle cores have been seen in the pedicle valve of *B. faringdonense* and, except in the hinge teeth, there is no development of fibrous secondary shell.

The brachial lobe canopies of *E. imperfecta* are very similar to those of thecidellinids such as *Thecidellina blochmanni* Dall. *T. blochmanni* may be distinguished by its much smaller, incipiently trilobed cardinal process. In *Eothecidellina* the posterior projecting spur (Text-fig. 6C) may be the precursor of the much more prominent posterior extension of the *Thecidellina* brachial lobe skeleton (Text-fig. 6D). *E. imperfecta* has a brachial valve microstructure which is closely comparable with the strongly suppressed fibrous secondary shell succession of *Thecidellina barretti* (Davidson),



TEXT-FIG. 5. Drawings to show brachial, lateral and posterior views of dorsal cardinalia. A–C, *Eotheidellina imperfecta* (Nekvasilová). D–F, *Bifolium faringdonense* (Davidson). G–I, *Bosquetella campichei* (de Loriol). Abbreviations: c.p., cardinal process; i., interarea; l.a.s., lateral adductor muscle scar; m.s., median septum; s., dental socket; v.c., visceral cavity. Scale bars represent 0.5 mm.

mapped by Williams (1973). In *T. barretti* the secretion of fibrous secondary shell is also strongly suppressed in the pedicle valve, in marked contrast to the well developed fibrous secondary layer found in *E. imperfecta*.

It is probable that the specimens alleged to be juveniles of *Backhausina schlueteri* (Lundgren) and *Backhausina groenwalli* (Nielsen) figured by Pajaud (Pajaud 1970, p. 221, figs aa and cb) are assignable to *E. imperfecta*. However, because of their different age (*B. schlueteri*, Campanian; *B. groenwalli*, Danian) and geographical occurrence, they are not included in the synonymic list. In view of what is now known about ontogeny the specimens are, nevertheless, clearly separable from *Backhausina*, which destroys the argument for the neotenous derivation of *Thecidellina* from *Backhausina* (Pajaud 1970).

The differences in morphology, microstructure and stratigraphic occurrence are thought to be indicative of the taxonomic separation of *Eotheidellina* and *Thecidellina*, but similarities, particularly in the development of the brachial lobes (Text-fig. 6C, D), are thought to imply a close phylogenetic relationship. Similarly, the new evidence indicates that *Eotheidellina* and *Bifolium* are phylogenetically related. Although morphologically distinct, the similarity of the brachial lobes is

EXPLANATION OF PLATE 4

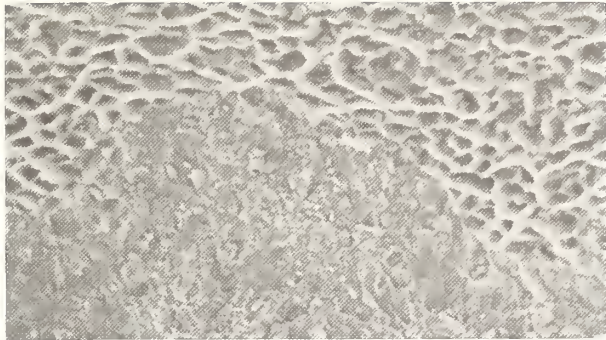
Figs 1–7. *Eotheidellina imperfecta* (Nekvasilová). 1, BD 9024/4; section through the free ventral wall of the pedicle valve, showing the general shell fabric and invaginated granular calcite in longitudinal section (section orientation – horizontal, almost parallel with the shell surface; section location – anterior sector), $\times 200$. 2, BD 9023/33; section through the free ventral wall, showing the fibrous secondary shell and invaginated granular calcite in transverse section (section orientation – parallel with the plane of the commissure; section location – anterior sector), $\times 700$. 3, same specimen; showing invaginated granular calcite almost pinched off to form a tubercle core, $\times 1000$. 4, enlarged portion of figure 1, as indicated; to show the junction between granular calcite and fibrous secondary shell in detail, $\times 1200$. 5, as figure 4; but showing detail of the convergence of fibrous secondary shell to pinch off granular calcite in the formation of a tubercle core, $\times 400$. 6, uniform granular calcite in the median septum of the brachial valve, $\times 3000$. 7, BD 9023/48; transverse section through the free ventral wall showing the succession of tubercle cores, stacked to form a median ridge (section orientation – parallel with the plane of the commissure; section location – anterior sector, mid-line of shell), $\times 250$.

Fig. 8. *Bosquetella campichei* (de Loriol). 42530/23; section through the brachial valve showing acicular calcite tubercle cores in transverse section (section orientation – parallel with the plane of the commissure; section location – antero-lateral sector), $\times 700$.

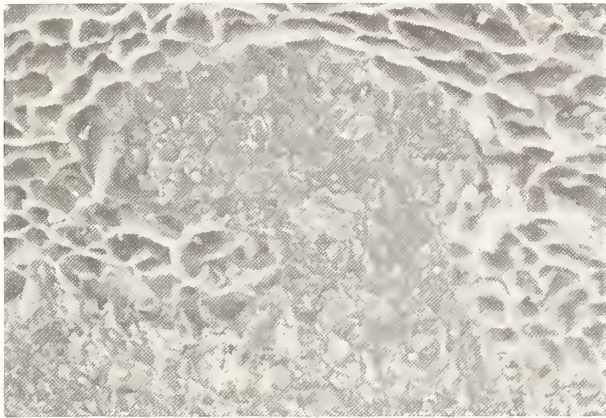
All scanning electron micrographs of gold-coated cellulose acetate peels of sectioned specimens.



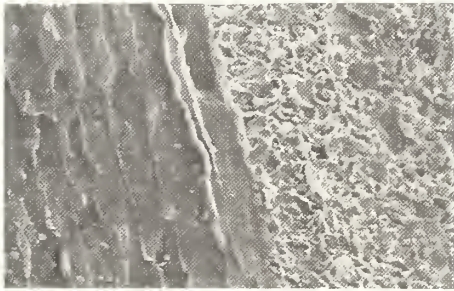
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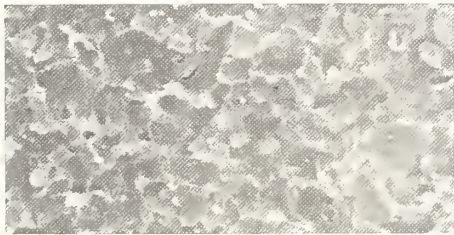
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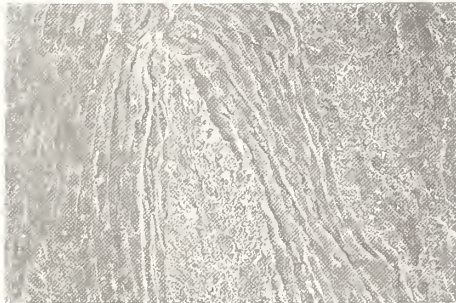
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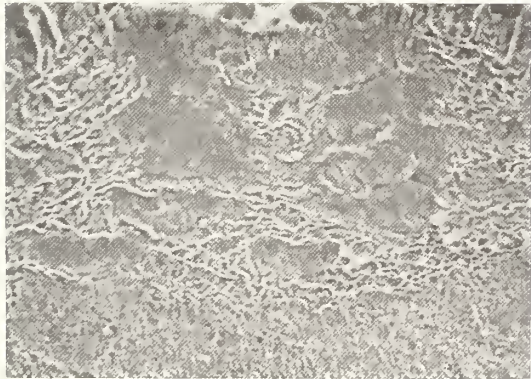
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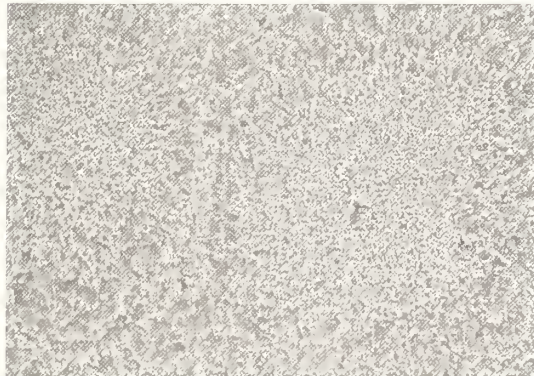
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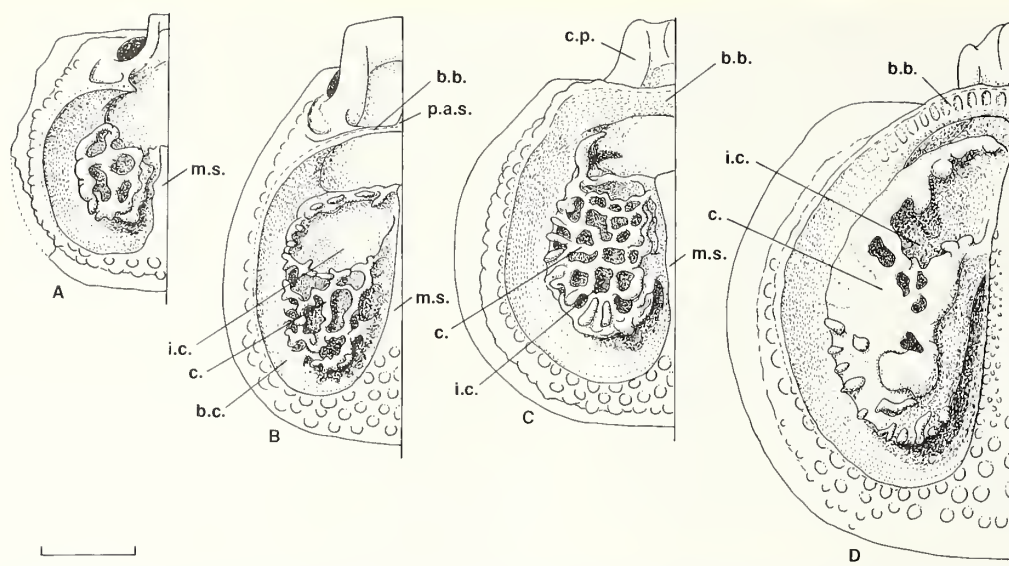
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TEXT-FIG. 6. Diagrams to show the possible sequence (A–D) in the development of canopied brachial lobes. A, *Moorellina dubia* (d'Orbigny), Aalenian, drawn from specimen BD 9028. B, *Bifolium faringdonense* (Davidson), Upper Aptian, reconstructed from specimen BD 9026. C, *Eothecidellina imperfecta* (Nekvasilová), Upper Cenomanian, reconstructed from specimen BD 9024. D, *Thecidellina blochmanni* Dall, Recent, after Nekvasilová (1967, pl. 6, fig. 1). Abbreviations: b.b., brachial bridge; b.c., brachial cavity; c., brachial lobe canopy; c.p., cardinal process; i.c., intrabrachial cavity; m.s., median septum; p.a.s., posteriorly arching spur.

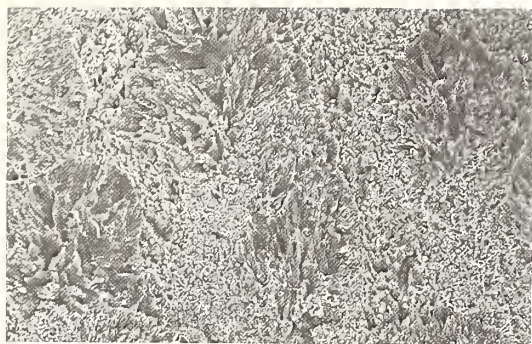
Scale bar represents 0.5 mm.

again striking. Its earlier occurrence (Upper Aptian) and the less complete development of the canopies of the brachial lobes (Text-fig. 6B) places *Bifolium* in an attractive position from an evolutionary point of view. However, the heavily suppressed fibrous secondary mosaic of the pedicle valve seems to rule out *Bifolium* from a direct ancestral position. Pajaud (1970) regarded *Rioulina* as being ancestral to *Bifolium*. Smirnova (1984) considered *Rioulina* to be close to, but, slightly off the main line of *Bifolium* descent from *Moorellina* stock. Smirnova's interpretation is probably more accurate, since it can now be demonstrated that the small, Middle Jurassic (Aalenian) *Moorellina*

EXPLANATION OF PLATE 5

Figs 1–8. *Thecidiopsis tetragona* (Roemer). 1, 42532/3; inner surface of the primary layer showing acicular crystallites of future tubercle cores 'seeded' on to granular calcite (section orientation – parallel with the external shell surface; section location – antero-lateral sector), $\times 350$. 2, same specimen; showing acicular crystallite tubercle cores developed but still separated by granular calcite, $\times 350$. 3, 42533/49; transverse section through the free ventral wall showing the attenuated fibrous strands at the inner boundary (lower margin) and transversely sectioned tubercle cores (section orientation – parallel with the plane of the commissure; section location – as fig. 1), $\times 375$. 4, same specimen; showing tubercle core in greater detail, $\times 800$. 5, enlarged portion of figure 4; showing the development of scalenohedra-like bodies (lower left) in the axial region, $\times 4000$. 6, 42533/49; attenuated strand showing detail of fibrous secondary shell in transverse section (section orientation and location as in figure 3), $\times 400$. 7, 42533/7; oblique section through the free ventral wall showing the acicular crystallite tubercle cores in lateral contact (section orientation and location as in figure 3), $\times 325$. 8, same specimen; showing the characteristic 'fish-scale' overlap of acicular crystallite tubercle cores in oblique section, $\times 250$.

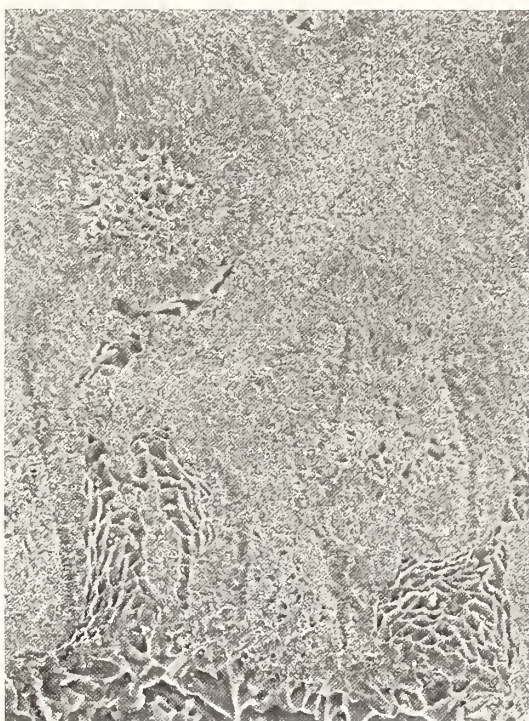
All scanning electron micrographs of gold-coated cellulose acetate peels of sectioned specimens.



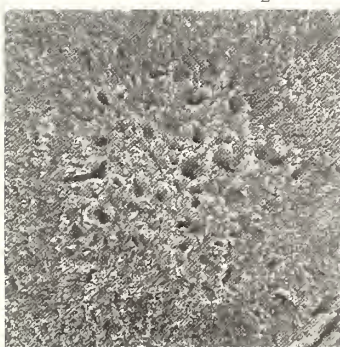
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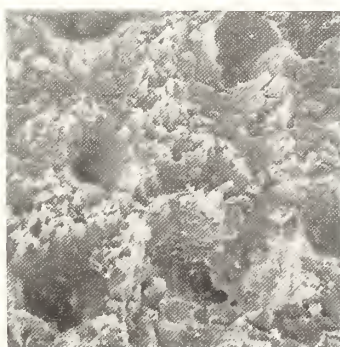
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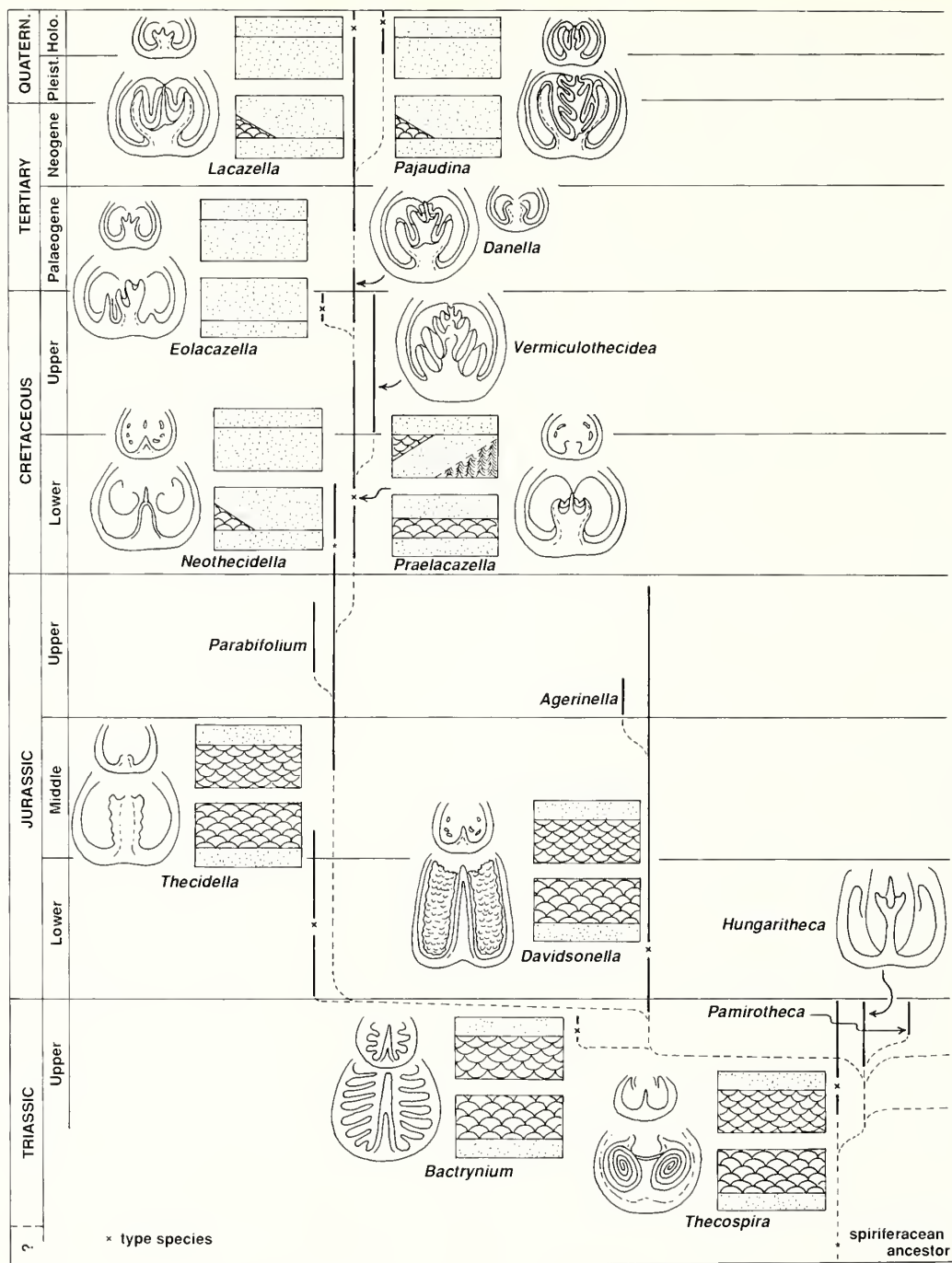
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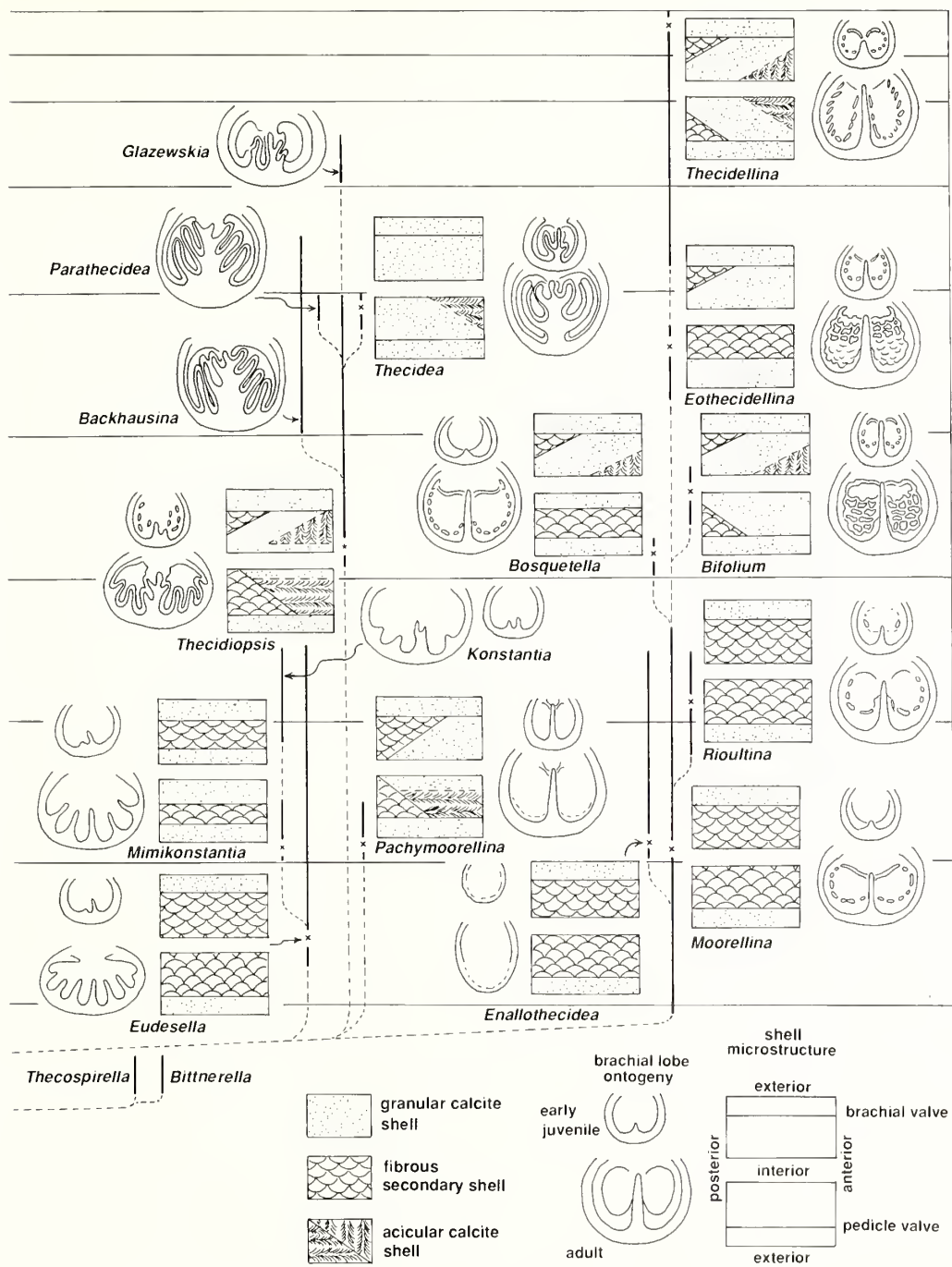


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TEXT-FIG. 7. Phylogenetic reconstruction, showing, where known, the essential ontogeny of the brachial supports, and, shell microstructure of thecalidinae genera. In the diagrammatic illustrations of shell microstructure, horizontal lines indicate continuous layers, diagonal lines indicate restricted distribution. The presence of periostracum is assumed in all genera.

dubia possessed brachial structures (Pl. 2, figs 7–9; Text-fig. 6A) which may be regarded as rudimentary canopied brachial lobes (Pl. 3, fig. 8), in the early stages of their evolution. The shell microstructure of *M. dubia* is typically moorellinid (Pl. 3, fig. 9). Smirnova's (1969) discovery that the ontogeny of *Thecidiopsis* did not pass through a rioultinid phase (undivided median septum and auriform brachial lobes (Pajaud 1966, p. 630)) clearly separates *Eothecidellina* from *Thecidiopsis*.

The distribution of secondary fibrous shell in *E. imperfecta* and *T. tetragona* is instructive. Although fibrous secondary shell forms a continuous thin sheet in the pedicle valve of *E. imperfecta*, its appearance coincides with the beginning of the development of the free ventral wall. In *T. tetragona* the residual strands of fibrous secondary shell appear at the inner boundary of the free ventral wall, after substantial deposition of acicular calcite. The diagram of *T. tetragona* shell microstructure in Smirnova's (1979) paper is misleading because the fibrous secondary layer is depicted as a well-differentiated, continuous internal layer. The seeding of patches of acicular crystallites on to the inner surface of the primary layer is very reminiscent (see Williams 1968, p. 7, text-fig. 4) of the initiation of normal secondary fibres. In both genera the sudden appearance of fibrous secondary shell, suggests a latent ability of the epithelial cells to switch from the secretion of acicular crystallites, to the secretion of normal secondary fibres. As already noted, the acicular crystallite tracts discovered in *Pachymoorellina*, and well established in *T. tetragona*, equate with the rod-like bodies of Smirnova (1979, 1984) not, as previously stated (Baker 1989, p. 67), with the fir-tree structures.

Thecideidine phylogeny

The various phylogenetic models proposed for the Thecideidina have been thoroughly reviewed in a recent paper (Baker 1990) and need only brief further mention here. The earlier interpretations of Elliott (1948, 1953) and Backhaus (1959) were modified by Rudwick (1968), Smirnova (1969) and Pajaud (1970). Although the rectilinear evolutionary pattern of the Lacazellinae had been well understood for some time (Pajaud 1970) the evolution of the Thecidellinidae and Thecideinae had remained problematical. Smirnova's (1969) demonstration of the distinctiveness of thecidellinid and thecideid ontogenetic development patterns revived interest in Backhaus's (1959) idea of two phyletic groups, and introduced the notion of parallel lineages within the groups. Smirnova's (1969) interpretation, with additional refinement (Smirnova 1984), was much more satisfactory, since it avoided most of the problems (Baker 1990, pp. 177, 180) of heterochronous expression, mutation, neoteny and undiscovered adults attendant to the other schemes. Williams's (1973, p. 468, fig. 100) phylogenetic chart of thecideidine shell structure variation had been modelled on the phylogenetic framework proposed by Pajaud (1970). Subsequent studies (Baker and Elston 1984; Smirnova 1984; Baker 1989) showed that Pajaud's phylogeny was flawed. Also, the suppression of fibrous secondary shell occurred much earlier in the history of the group than Williams envisaged. Interpretation of the new morphological and microstructural evidence obtained from the current study of *E. imperfecta*, *B. faringdonense*, *B. campichei* and *M. dubia*, not only strengthens the lineages identified by Smirnova (1984), but also enables a clearer understanding of the phylogeny of thecidelliniform genera to be reached. Similarly, the new interpretation of the shell microstructure of *T. tetragona*, allied to the evidence from study of *Mimikonstantia sculpta* Baker and Elston, 1984, and *P. dumdriensis* (Baker 1989), gives a much clearer picture of lineage within the Thecideinae.

My review of existing taxonomic and phylogenetic models (Baker 1990) clearly stated the case for including thecospiraceans and *Bactrynum* in the Thecideidina and supported the view of Dagis (1973) that early thecospiraceans were very close to thecideidine ancestral stock. I concluded that sufficient information was available to enable a reliable taxonomic and phylogenetic framework to be established. A revised classification was presented, including the Thecospiracea and the Bactryniidae in the Thecideidina which, in turn, was included in the Spiriferida. A recent study (Benigni and Ferligi 1989), assigning Carnian thecospirids from Italy to the Strophomenida, failed to address the arguments advanced by Williams (1973) and Baker (1984) in favour of removal of the Thecospiracea to the Spiriferida. In content, if not conclusion, the study confirms the very close relationship between thecospiracean and thecideacean shell microstructure and strengthens the

argument for inclusion of the Thecospiracea in the Spiriferida, because the microstructure of the so-called taleolae of *Thecospira semseyi* Bittner, 1912, is so close to the microstructure of the denticles of juvenile spiriferaceans (compare Benigni and Ferliga 1989, p. 527, fig. 9b, with Baker 1984, pl. 77, fig. 3) as to almost be interchangeable.

Proposals about phylogeny were deferred (Baker 1990, p. 183; research in progress) pending the interpretation of new morphological and microstructural evidence. The evidence from the current study, incorporated into the existing framework, now enables a revised phylogeny to be presented (Text-fig. 7). Shell microstructure must not be regarded as diagnostic in every case. For example, although uniformity of shell microstructure is characteristic of the various species of *Moorellina*, shell microstructure varies in *Thecidiopsis*. Williams's (1973, p. 465) study of *T. essenensis* indicated a more heavily suppressed fibrous secondary mosaic than that found in *T. tetragona*. In *T. essenensis*, fibrous shell is found in the hinge teeth and base of the outer wall of the hemispondylium but, unless overlooked, is absent from the free ventral wall. Therefore, although considerable variation of shell structure may be found among species assigned to a particular thecideidine genus, the status of observed differences remains uncertain. It is clear, however, that the range of shell microstructure differences reflects the operation of biologically distinct physiological processes, which are probably no less diagnostic than differences in morphology. Nevertheless, in the absence of quantifiable morphological variation, it would be premature to identify morphogenera solely on the basis of shell microstructure. Therefore, in the current study shell microstructure of the genera is illustrated in so far as is possible by that of the type species (Text-fig. 7).

CONCLUSIONS

It is clear that ideas about morphology of the brachial lobes of species such as *E. imperfecta* and *B. faringdonense*, based solely on interpretation of broken skeletal supports as seen in separated brachial valves, may lead to confusion over the systematic arrangement of taxa. The current study further emphasises the critical importance of the study of serially sectioned whole shells in the determination of the form of thecideidine brachial lobes, because the often distinctively sculptured structures, arising from differential shell accretion and resorption, are almost invariably destroyed in separated valves.

As for shell microstructure, the essential limitation of morphogeneric taxonomic or phylogenetic frameworks remains the inability to incorporate distinctions which may be perfectly valid biogenerically, but remain undifferentiated at morphogeneric level. However, in the Thecideidina, chronologically arranged changes in shell microstructure and microstructures persistent over long periods become important indicators of lineage, especially when allied to morphological and ontogenetic evidence.

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THE FIRST DICYNODONT FROM THE LATE PERMIAN OF MALAGASY

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ABSTRACT. Until now, no therapsid was known with any certainty from Malagasy. The present specimen, discovered in 1948, but never described, is the first record of a complete dicynodont skull from this country. A description of the skull is given and it is referred to a new species of the genus *Oudenodon*. The rarity of dicynodonts in Malagasy may be because of environmental differences from the adjoining landmass of Africa.

RESUMÉ. La présence de thérapside à Madagascar n'avait jamais été montrée avec certitude. Le présent spécimen, collecté en 1948 mais jamais décrit, est la première découverte d'un crâne presque complet de dicynodonte dans cette région. Une description du crâne en est donnée et il est attribué à une nouvelle espèce du genre *Oudenodon*. La rareté des dicynodontes à Madagascar peut être due aux conditions de milieu, différentes de celles régnant sur la masse continentale africaine contiguë.

THE Permo-Triassic of Malagasy, sometimes called the 'Malagasian Karoo' is known for the richness of its fossils which have been found in reptile-bearing nodules from the Lower Sakamena Formation (Late Permian), (Piveteau 1926, 1957; Carroll 1981; Currie 1981). Reptiles, such as *Hovasaurus*, *Thadeosaurus*, *Tangasaurus*, and *Claudiosaurus*, are well represented and constitute a typical Malagasian fauna, unknown elsewhere. Until now, except for a fragmentary and unpublished specimen noted by Piveteau (1957), from below the *Cistecephalus* zone and provisionally referred to as a therapsid, the therapsids did not seem to be represented in this fauna. The abundance of diapsids and the rarity of therapsids characterize the Malagasian Karoo in comparison with the South African Karoo, where therapsids are abundant. However, the study of a new specimen, housed in the collections of the Université Paris 6, confirms the presence of therapsids in the Late Permian of Malagasy.

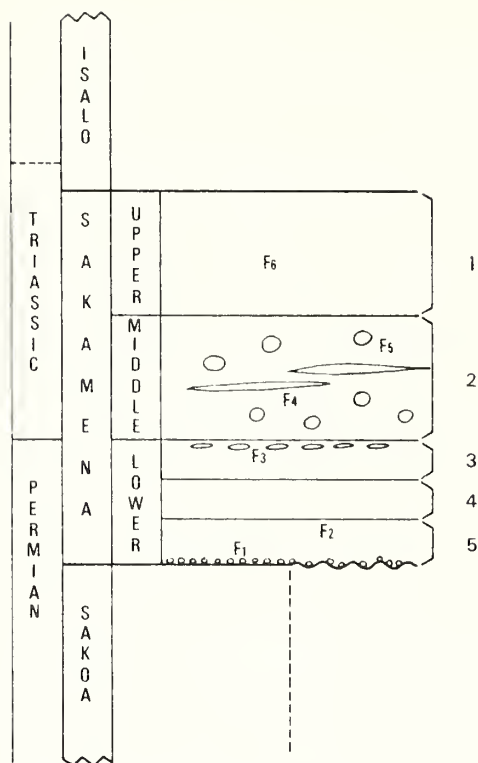
THE MATERIAL

Locality and material

The specimen was collected in 1948 by François Tortochaux, a French geologist then working for the Malagasian Petroleum Company. It consists of a partially crushed skull, coming from a locality whose exact position is unknown, between Ranohira and Benenitra (south Malagasy). The skull was in a calcareous nodule from the upper part of the psammitic sandstone constituting the latest part of the Lower Sakamena Formation (Late Permian) (Text-fig. 1). The matrix has been removed by acid processing. The skull is nearly complete, but dorsoventrally crushed with a broken skull roof (Text-fig. 2). The bone surface is weathered and sutures are indistinct. The anterior part of the snout is slightly distorted by shear, and the posterolateral part of the right temporal fenestra is preserved only as a film of bone. The total length of the specimen is 160 mm, and the maximal width is 95 mm. The lower jaw is mostly complete and preserved *in situ*. The lateral bones of the right ramus and of the posterior part of the left ramus are missing. In the palate, the pterygoids and right basioccipital tuber are visible. The anteriormost part of the palate is not visible. The atlas, axis and three succeeding vertebrae are also preserved.

Description

In dorsal view, the pre-orbital region is short in comparison with the post-orbital, even allowing for distortion (Text-fig. 3a). The *postorbitals* are large and rise to form a low sagittal crest ending at the level of the pineal foramen. Anteriorly, they are separated by a small shield-shaped *preparietal*. They constitute the anterior and



TEXT-FIG. 1. Stratigraphical scale of the Sakamena Formation, with locations of the different fossil levels. 1, clays and sandstone called 'Upper continental red level'; 2, *Septaria* clays with interbeds of sandstone; 3, psammitic sandstone; 4, clays with gypsum; 5, sandstone and conglomerate. F1, small amphibian and reptile bones; F2, nodules with reptiles; F3, shales with *Glossopteris*, *Voltzia*...; F4, lens of sandstone with small amphibian and *Saurichthys* remains; F5, nodules with fishes; F6, rare plant remains. The dicynodont fossil comes from the level F2.

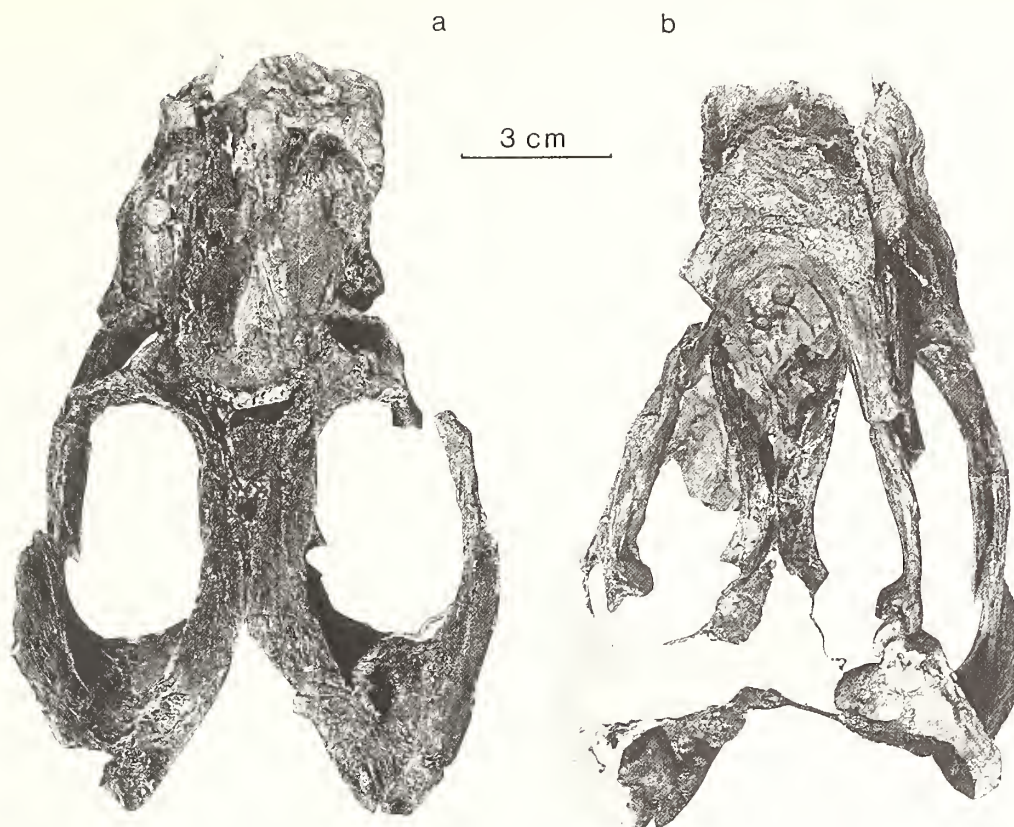
medial border of the temporal fenestrae, and all of the posterior edge of the orbital opening. The *squamosals* are very large, forming the posterior and lateral borders of the temporal fenestrae. Because the skull roof is damaged, the *postfrontals* are not visible, but their impression persists as a depression. They were elongated, with a triangular shape, and seem to have contacted only the postorbitals. The left *prefrontal* persists as an elongated bone bordering the anterosuperior edge of the orbital opening. The *frontals* seem to be large, but their anterior limits cannot be determined. Likewise, the narinal area cannot be observed because of the anterior distortion and loss of the snout. The measurements of the temporal fenestrae are as follows: left: length, 58 mm; width, 30 mm; right: length, 59 mm; width, 31 mm.

In lateral view, the general outline of the skull is modified by the dorsoventral crushing (Text-fig. 3c). The specimen is totally edentulous. The *maxilla* is large and extends vertically. The *jugal* is anteroposteriorly elongated, forming the inferior and posterior edges of the orbital opening. The *mandible* is strong, with a thick and high anterior part composed of the *dentary*. Posteriorly, the mandible is thinner. The *articular* is divided into lateral and median articulatory condyles.

The ventral view is more difficult to observe (Text-fig. 3b). The palate is largely damaged, and the postero-lateral part of the skull is destroyed. The mandibular symphysis is strong and anteriorly extended. Conversely, the posterior part of each ramus is narrow.

Identification

The short snout, elongate temporal fenestra, large laterally-expanded squamosal, and distinctive articular confirm that this specimen is a dicynodont. Among the dicynodonts, this specimen can be compared with the four main Permian genera: *Dicynodon*, *Oudenodon*, *Diictodon* and the rare *Kingoria* (Cluver and Hotton 1981). Because of the lack of a caniniform tusk, it cannot belong to *Dicynodon*. The absence of the distinctive square caniniform process indicates that the specimen does not belong to the genus *Diictodon*. To distinguish between *Oudenodon* and *Kingoria*, it is necessary to know the state of certain characters of the lower jaw, in particular whether a dorsal dentary sulcus is present or not. The present specimen does not have the anterior dorsal surface of the jaw ramus completely exposed, but the dorsal edge of the dentary which is visible is sharp-edged



TEXT-FIG. 2. *Oudenodon sakamenensis*, Late Permian, south Malagasy. Type specimen, PVHR 288. *a*, Dorsal view; *b*, ventral view.

as would be expected of the medial wall of a dorsal dentary sulcus, as present in *Oudenodon*. Another feature which indicates an assignment to *Oudenodon* is the suggestion of a large palatal exposure of the palatine bone. This would be small in *Diictodon* and *Kingoria*.

King (1988) lists three species of *Oudenodon*. The genotype is *Oudenodon bainii* Owen, 1860, known from South Africa. *O. grandis* (Haughton 1917) is also from South Africa, while *O. luangwensis* (Boonstra 1938) is known from Zambia (Keyser 1975).

The present specimen presents two features which distinguish it from the known species of *Oudenodon*. First, the lateral dentary shelf is drawn up into a pronounced boss anteriorly which is continued postero-ventrally as a sharp ridge (Text-fig. 3c). Secondly, the posterior edge of the mandibular fenestra is drawn up into a blunt ridge oriented antero-ventrally, forming an anterior shelf to the reflected lamina of the angular (Text-fig. 3c). On account of these features the present specimen is assigned to a new species of *Oudenodon*.

SYSTEMATIC PALAEOONTOLOGY

Suborder ANOMODONTIA Owen, 1859

Infraorder DICYNODONTIA Owen, 1859

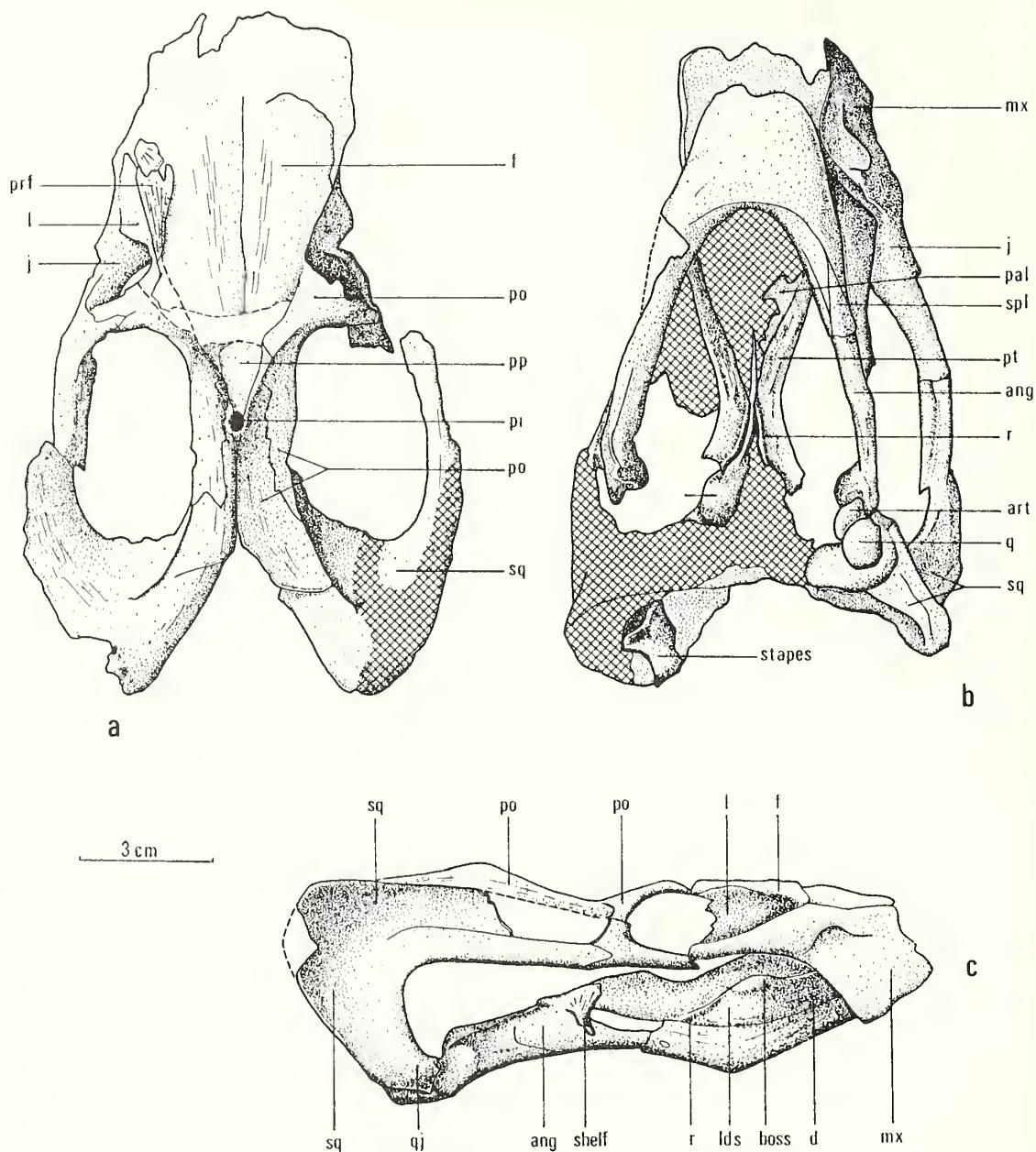
Superfamily PRISTERODONTOIDEA Cluver and King, 1983

Family DICYNODONTIDAE Cluver and King, 1983

Subfamily CRYPTODONTINAE Owen, 1859

Genus *Oudenodon* Owen, 1860

Diagnosis. Given by King (1988).



TEXT-FIG. 3. *Oudenodon sakamenensis*, Late Permian, south Malagasy. Type specimen PVHR 288. *a*, Dorsal view; *b*, ventral view; *c*, right lateral view.

Oudenodon sakamenensis sp. nov.

Text-figures 2 and 3

Etymology. From Sakamena, the name of the Formation and of the river which crosses this area.

Holotype. Nearly complete skull, PVHR 288, preserved at the Laboratoire de Paléontologie des Vertébrés de l'Université Paris 6.

Type locality. Between Ranohira and Benenitra, South-western Malagasy.

Horizon. Top of the Lower Sakamena Formation, Late Permian.

Diagnosis. Medium to small member of the genus, skull longer than broad. Lower jaw with lateral dentary shelf drawn up into a boss anteriorly and extending postero-ventrally as sharp-edged ridge; reflected lamina of angular bearing a pronounced blunt shelf anteriorly.

PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

Dicynodonts are known from South Africa, eastern Africa, Morocco, India, China, Antarctica, Europe, USSR, and North and South America, but until now had not been reported from Malagasy. *Oudenodon* is known from South Africa, Zambia and, now, Malagasy. In South African localities, dicynodonts are very abundant fossils, and *Oudenodon* is a common genus from *Cistecephalus* Zone localities, and even more so in the succeeding *Daptocephalus* Zone (King 1986). It is therefore puzzling that these abundant therapsids should be found so rarely in the otherwise reptile-rich fauna of Malagasy.

Two alternative explanations present themselves. First, that Malagasy was separated from South and East Africa by some kind of barrier (sea, mountain) during the Late Permian, preventing easy migration of dicynodonts to Malagasy. In this case, an impoverished dicynodont fauna, composed of species very distinct from the mainland forms, would be expected. This explanation can be dismissed for two reasons. First, it is known that Malagasy was part of the same landmass as Africa during the Late Permian. There was no ocean barrier to migration, and no evidence of other kinds of barrier. Secondly, although the present Malagasian dicynodont is specifically distinct from mainland African forms, it is not particularly different, and no more different than is the Zambian *Oudenodon* from the South African.

The second explanation to account for the rarity of therapsids in Malagasy is that the conditions of fossilization there were very different from those in South Africa. This has been suggested by Piveteau (1926), Currie (1981) and Carroll (1981). This would imply that the habitats in which dicynodonts and other therapsids were abundant in South Africa were not those habitats which have been sampled in the Malagasian sediments. There are some indications that some of the Malagasian diapsids coming from the same locality (*Hovasaurus*, *Claudiosaurus*) were aquatic or semi-aquatic (Currie 1981; Carroll 1981; de Buffrénil and Mazin 1989), and it may, therefore, be that dicynodonts were occupying more terrestrial environments which are not sampled in these Malagasian localities. By contrast, South African localities, where no similar small diapsid assemblages are known, may represent the more terrestrial (or less aquatic) habitats. Further sedimentological and palaeontological sampling of contemporaneous localities in Malagasy, and functional anatomical study of the fossils they contain, is needed before this conclusion can be substantiated.

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ABBREVIATIONS USED IN TEXT-FIGURES

ang: angular; art: articular; b.o.t.: basioccipital tuber; d: dentary; f: frontal; FT: temporal fenestra; j: jugal; l: lachrymal; l.d.s.: lateral dentary shelf; mx: maxilla; ORB: orbital opening; pal: palatal; pi: pineal foramen; po: postorbital; pp: postparietal; prf: prefrontal; pt: pterygoid; q: quadrate; qj: quadratojugal; r: ridge; spl: splenial; sq: squamosal.

AN ONTOGENETIC SEQUENCE OF COCCOLITHS FROM THE LATE JURASSIC KIMMERIDGE CLAY OF ENGLAND

by JEREMY R. YOUNG *and* PAUL R. BOWN

ABSTRACT. The Kimmeridge Clay of Kimmeridge Bay, Dorset, UK, includes several stone bands which electron microscopy shows are coccolith limestones dominated by the species *Watznaueria fossacincta*. The assemblage includes not only fully grown coccoliths but also specimens at earlier growth stages, including proto-coccolith rings. A complete ontogenetic sequence can thus be reconstructed. This interpretation is supported by the occurrence of early growth stages inside coccospheres, i.e. intracellular coccoliths preserved in the process of growth. The coccolith formation process appears to have been directly comparable to that known in living coccolithophores. The early growth phases have previously been described as separate species; these can now be put in synonymy.

COCCOLITHS are minute calcareous platelets produced by unicellular planktonic algae of the division Prymnesiophyta. They are borne extracellularly as a coccosphere of several individual coccoliths, but are formed intracellularly, as the product of an elaborate biomineralization process. Studies of this process in living coccolithophores have highlighted the fact that it does not occur by calcification of a pre-existing organic matrix, but rather is a growth process. Typically coccolith growth involves first nucleation of a proto-coccolith ring of simple crystals, then closely regulated growth of these crystals into the complex segments that constitute fully formed coccoliths (Westbroek *et al.* 1984, 1989; Mann and Sparks 1988; van Emburg 1989; Young 1989). Since this is a growth process with distinct developmental stages, individual coccoliths can be considered to have an ontogenetic history. When this concept is contrasted with the alternative of regarding coccoliths as formed objects, it is clear that it can provide an improved framework for the interpretation of coccolith structure, morphological variation, classification and evolution. However, since the concept has been derived from study of a few living species, nannofossil palaeontologists have not been widely convinced of its relevance or applicability. We describe here, for the first time, an ontogenetic sequence of this type in the fossil record, and use it to illustrate the utility of such studies.

MATERIAL AND PALAEOENVIRONMENT

The Kimmeridge Clay Formation is a thick (c. 500 m) organic-rich shale of Late Jurassic age deposited over an extensive area of the NW European shelf including much of the North Sea and southern England. The best known outcrops are in Kimmeridge Bay, Dorset, the stratotype of the Kimmeridgian Stage. A remarkable feature of the formation is the presence of several bands of laminated limestone almost entirely formed of coccospheres and isolated coccoliths of the species *Watznaueria fossacincta* (Downie 1957; Noel 1973; Gallois and Medd 1979). The extensive occurrence of coccospheres, the lamination of the sediment, and the absence of admixed clay are almost certainly the result of rapid deposition in anoxic bottom waters, as also indicated by geochemical and macrofaunal evidence (Myers and Wignall 1987; Oschmann 1988). The domination of the assemblage by a single species is partly a reflection of the low diversity of Late Jurassic nannofloras but is also suggestive of a degree of ecological restriction. The combination of

low diversity, good preservation and abundant coccospheres made these beds attractive for a study of morphological variation within a single species. For this reason a special study was made of coccoliths from one of the best developed limestone bands, the White Stone Band, within the *Pectinatites pectinatus* Zone.

ONTOGENETIC SEQUENCE

A typical fracture surface of the White Stone Band is illustrated in Plate 1, fig. 1. This shows abundant coccoliths and coccospheres of the species *Watznaueria fossacincta* (Black, 1971) Bown in Bown and Cooper 1989. Rare specimens of species from a few other genera also occur (*P.m* and *Z.e* on Pl. 1, fig. 1). In addition, several coccoliths with broad central areas and narrow rims are visible (arrows in Pl. 1, fig. 1). These lack the well developed shields of *W. fossacincta* but have structural similarities and have been regarded as separate species of the genus *Watznaueria* (e.g. Grun and Zweili 1980). However, if a series of these forms from the open rings to typical *W. fossacincta* specimens is assembled, it is apparent that there is continuous variation between them. Two such sequences are shown in Plate 1, one in distal view (Pl. 1, figs 3–5) and the other in proximal view (Pl. 1, figs 6–9). The continuity of variation is primary evidence that the variation is intraspecific but the range of morphology is too great for preservational, ecophenotypic or genotypic variation of mature forms. A simple alternative interpretation of this sequence is that it is an ontogenetic growth sequence, and indeed it is closely comparable to growth sequences described from living species such as *Emiliania huxleyi* (Westbroek *et al.* 1984, 1989; van Emburg 1989). Further evidence is provided by the presence of broken coccospheres containing ring-like coccoliths (Pl. 1, figs 2 and 10). The occurrence of these coccoliths inside the coccospheres is unlikely to be coincidental since several examples were seen in the electron microscope, and in the light microscope single coccoliths were also often discernible inside entire coccospheres. For the purposes of comparison, scanning electron micrographs were taken of broken coccospheres of cultured *Emiliania huxleyi* (Pl. 1, figs 11 and 12). The analogy with the fossil specimens is plain. So rather than being a chance association, these ring-like coccoliths occurring within coccospheres are almost certainly examples of fossilized intracellular coccoliths preserved due to death of the cell during the process of coccolith formation. This in turn makes it only reasonable to interpret the series of coccolith morphologies as an ontogenetic sequence of coccolith growth stages.

EXPLANATION OF PLATE I

Scanning electron micrographs of *Watznaueria* specimens in the White Stone Band, and comparable specimens of the modern coccolithophore *Emiliania huxleyi*.

Fig. 1. Typical fracture surface showing how rock is almost entirely composed of *Watznaueria* coccoliths, either isolated or in coccospheres. Arrows, incompletely formed coccoliths. Coccoliths of other species: *Z.e.*, *Zeugrhabdotus erectus*; *P.m.*, *Polypodorhabdus madingleyensis*. $\times 2500$.

Fig. 2. Broken coccosphere with internal coccolith at early growth stage. The living cell would have occupied the space within the coccosphere, and the incomplete coccolith would have been forming within it. $\times 6500$.

Fig. 3. Very early growth stage/proto-coccolith ring, distal view, $\times 10200$.

Fig. 4. Mid growth, distal/oblique view, $\times 11500$.

Fig. 5. Complete coccolith, distal view, $\times 6900$.

Fig. 6. Very early growth/proto-coccolith ring, $\times 11500$.

Fig. 7. Early growth, proximal view, $\times 11500$.

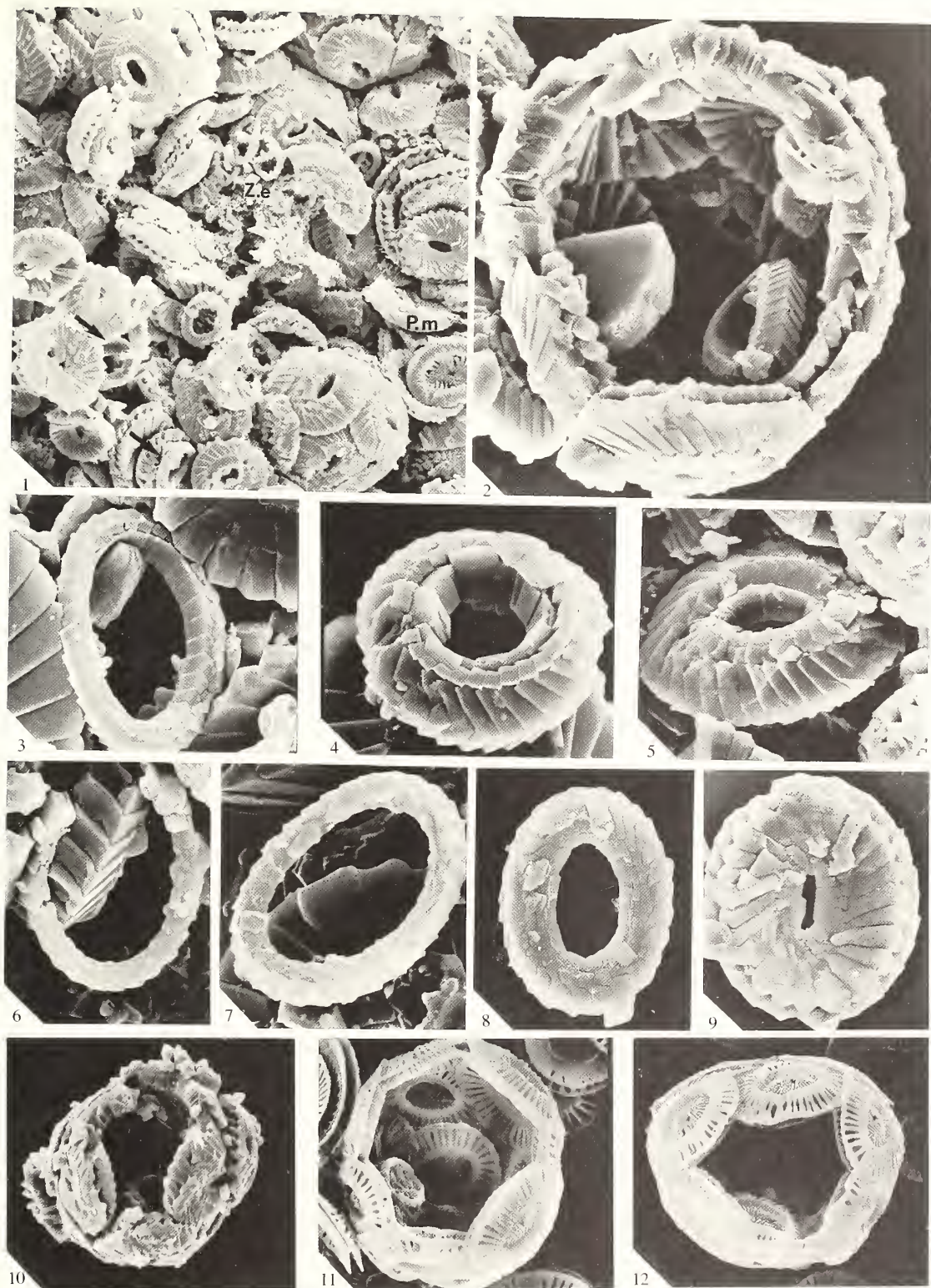
Fig. 8. Mid growth, proximal view, $\times 9300$.

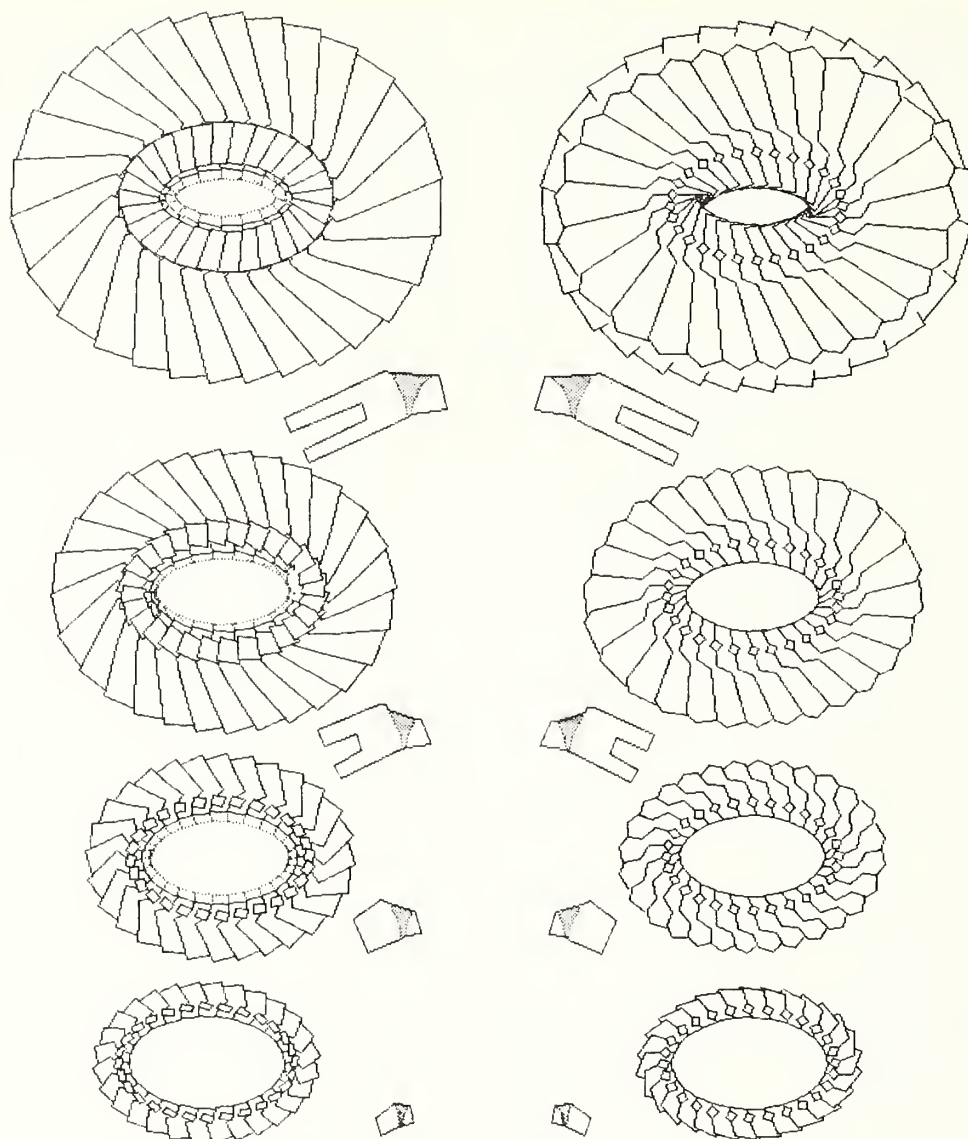
Fig. 9. Complete coccolith, proximal view, $\times 6900$.

Fig. 10. Broken coccosphere of *Watznaueria*, with internal proto-coccolith ring. This internal coccolith shows the earliest growth stage observed, $\times 3200$.

Fig. 11. Coccosphere of *Emiliania huxleyi*, grown in culture, showing internal proto-coccolith ring, $\times 6000$.

Fig. 12. Coccosphere of *E. huxleyi* showing internal coccolith, $\times 5100$.

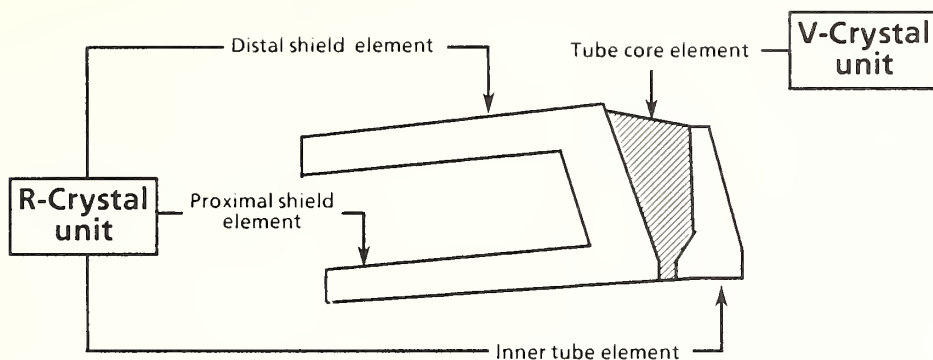




TEXT-FIG. 1. Growth stages of *Watznaueria*, based on a synthesis of observations on many specimens. Each growth stage is illustrated in distal view (left), cross-section (centre) and proximal view (right). Shaded portion of cross-sections is V-unit.

STRUCTURAL INTERPRETATION

An interpretative series of diagrams illustrating the growth sequence is given in Text-figure 1. Four growth stages are illustrated, each in proximal view, cross-section, and distal view. Terminology applied to the elements is explained in Text-figure 2. At the earliest observed stage the coccolith consists of an elliptical proto-coccolith ring of sub-quadrates crystals with intervening very small peg-like crystals. During subsequent growth these two sets of crystal units develop separately. They are referred to as the V- and R-crystal units (Text-fig. 2).



TEXT-FIG. 2. Terminology applied to the crystal units. The V-unit (shaded) has an approximately vertically directed crystallographic c-axis, and so is dark in cross-polarized light in plan view. The R-unit has radially directed c-axis and so is bright in cross-polarized light in plan view.

The larger, initially quadrate, R-crystal units develop into complexly shaped units, composed of several elements, and forming most of the coccolith. The *proximal shield elements* are formed by growth radially outward from the proto-coccolith ring. The elements have a slight initial counter-clockwise kink possibly due to change in growth direction after initial impingement of the crystals (Pl. 1, figs 6-9; Text-fig. 1, left side). The *distal shield elements* show the same kink, clockwise directed in this view, then growth with counter-clockwise precession (Pl. 1, figs 3-5; Text-fig. 1, right side). At the early growth stages the distal shield element directly overlies the proximal shield element, and they are united by a thickened outer tube cycle (Pl. 1, figs 2, 4, 7). Subsequent growth separates the proximal and distal shield elements since there is about a 30° difference in radial growth direction between them.

In proximal view the R-crystal units of the proto-coccolith ring can be seen to grow radially inward as well as outward, closing the central area. These elements also grow upward forming wedge-shaped *inner tube elements* (Pl. 1, figs 3-5; Text-fig. 1, centre).

The interstitial peg-like V-crystal units of the proto-coccolith ring develop upwards only, forming relatively simple crystals, composed of only one element. They outcrop on the distal surface of the complete coccoliths with the appearance of small rectangular plates, but root back to the proximal surface forming a core to the tube, and so are termed here *tube-core elements*.

The R- and V-crystal units remain distinct throughout ontogeny. They also are clearly separated during diagenesis. Under conditions of diagenetic secondary calcification (as in this material) different overgrowth crystal faces develop on the two types of units and there is no sign of them fusing; by contrast the proximal and distal shield elements of the R-crystal unit often do fuse. Under conditions of diagenetic dissolution the V-crystal units are often selectively etched, and may be entirely removed; this morphotype has occasionally been regarded as a separate species *Calolithus martelae* Noel, 1965. The consistent separation of the two crystal units indicates that they are discrete, separately nucleated cycles, presumably with different crystallographic orientations. The crystallographic orientation of the main units is readily determined by light microscope observations, using cross-polarized light and a gypsum plate (as described by Romein 1979). The c-axis is orientated along the length of the proximal shield elements, and so parallel to the base of the coccolith. This is also reflected in the prismatic overgrowths on these elements and in their termination by a zone of crystal faces (Pl. 1, figs 2 and 9). The optical orientation of the V-crystals is less easily determined, but careful light microscope observation of side views suggests the c-axes are directed approximately perpendicular to the base of the coccolith, i.e. at 90° to the c-axes of the main units. In plan view this is indicated by the tube-core cycle appearing as a dark ring in cross-polarized light.

COMPARISON WITH LIVING SPECIES

Information on coccolith growth is available for a number of living species. Comparison of these species suggests that all the heterococcolith rims show a similar pattern of development (Young 1989; Westbroek *et al.* 1989). Holococcoliths and the central area structures of some heterococcoliths appear to develop in different ways, but *Watznaueria* coccoliths are straightforward heterococcoliths, and so should be directly comparable with the living species. The principal points of similarity between coccolith formation in the living species and their applicability to *Watznaueria* are as follows:

1. Calcification is intracellular (Pl. 1, figs 11 and 12). In *W. fossacincta* the partially formed coccoliths inside coccospheres are striking evidence of this (Pl. 1, figs 2 and 10).

2. Nucleation occurs as a single event – around the rim of an organic base-plate producing a proto-coccolith ring of simple crystals. Proto-coccolith rings are figured here for *W. fossacincta* (Pl. 1, figs 1, 3, 6, and 10). The original presence of an organic base-plate can only be inferred.

3. Crystal growth proceeds upward and laterally from the proto-coccolith ring so that it remains on the proximal surface of the coccolith. This is precisely the pattern of growth seen here.

4. All the crystal units of a single cycle develop according to a single plan, although in some cases to differing degree. *Watznaueria* is a typical coccolith in this respect.

5. Individual crystal units are of complex form but there are rather few separate sets of crystal units. *W. fossacincta* is a fine example of this; superficial examination might suggest that the various cycles of elements were all discrete crystallites but in fact most of them unite, to form the R-crystal units, leaving only the V-crystals separate – as shown here and argued earlier (Bown 1987).

The most distinctive feature of the *Watznaueria* structure is the double proto-coccolith ring and development of a tube-core cycle. This does not have an obvious analogue in the coccoliths of the best studied species, *Emiliania huxleyi*, but does in several other species, for instance *Coccolithus pelagicus* (Young 1989; Steinmetz and Young unpublished data) and *Pleurochrysis carterae* (Outka and Williams 1971). Thus the morphological development of this Mesozoic coccolith was directly comparable to that of living species, and there is no reason to believe that qualitatively different biochemical processes were involved.

TAXONOMIC IMPLICATIONS

The most immediate application of these observations is that they allow a simplification of Mesozoic nanofossil taxonomy. A number of species of *Watznaueria*/*Ellipsagelosphaera* (a subjective junior synonym) have been proposed based on the degree of opening of the central area and on shield width. On the basis of the growth sequence worked out here, these forms can be seen to be simply growth stages. They include: *E. strigosa* Grun and Zweili, 1980 – proto-coccolith ring; *E. tubulata* Grun and Zweili, 1980 – early growth stage; and *W. ovata* Bukry, 1969 – late growth stage.

Complications are introduced by the presence of forms with a disjunct bridge in the central area (*W. britannica*, and its growth stages *W. lucasii* and *W. reinhardtii*) and by an evolutionary trend toward forms with entirely closed central areas (*W. barnesae*). With the clarification of the structure provided by understanding the growth sequence, and the resultant reduction in number of taxa it should, however, be possible to deal with the genus as a coherent lineage. This in turn should allow meaningful description of its evolutionary development and allow the definition of biostratigraphically useful trends. This would be a considerable contribution to Mesozoic nanofossil biostratigraphy since *Watznaueria* species are the most common component of nanofossil assemblages from the Upper Jurassic to the end Cretaceous plankton extinctions.

Our observations are also significant for higher taxonomy and the relationships between nanofossil families. Rim structure has long been recognised as a primary criterion of higher classification (e.g. Perch-Nielsen 1971; Romein 1979; Bown 1987). However, without a clear understanding of how rim structures develop during ontogeny, their description and interpretation

has been confused. The growth model provides such a framework, and highlights the importance of identifying crystal unit cycles and their crystallographic orientation. In this specific case the identification of a double proto-coccolith ring and determination that the tube cycle has a quite different optical orientation to that of the main units permits a number of hypotheses as to the relationships of Mesozoic coccoliths to be made. These are currently the subject of active investigation.

PALAEOECOLOGICAL SIGNIFICANCE

Incomplete coccolith morphotypes have not been widely reported from the fossil record, even when they have been described as separate species. Probably this is mainly because they are somewhat inconspicuous in the light microscope or easily dismissed as preservational artefacts. If they are specifically looked for they can be found in most coccolith assemblages. Nonetheless their abundance in the White Stone Band does seem unusually high, for either fossil or living coccolith assemblages. Culture work on the living species *Emiliania huxleyi* provides one possible interpretation. Incomplete coccoliths are most common in samples from the logarithmic growth phase of cultures grown in high nutrient media (Young unpublished data). An ecological analogue for this situation might be bloom conditions. Such conditions have been independently suggested for the *pectinatus* Zone of the Kimmeridge Clay, in order to explain the coincidence of high productivity, monospecific assemblages and anoxic conditions (Gallois 1976). Possibly the high occurrence of early growth stages may constitute a useful indicator of blooms.

CONCLUSION

Evidently coccolithogenesis occurred in the Jurassic by processes very similar to those acting today. In consequence information on the process derived from study of living coccolithophores can be applied to the study of fossil coccoliths. This can have useful applications in understanding taxonomy and evolution, and possibly in making palaeoecological interpretations. More generally it helps provide a palaeobiological perspective to coccolith research, which has been rather dominated by biostratigraphy. Also, understanding the ontogenetic growth of coccoliths allows the application of basic evolutionary concepts such as heterochrony to coccoliths. Since coccoliths have one of the best fossil records of any group this should enrich evolutionary studies as well as coccolithophore research.

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AMINO ACIDS FROM FOSSILS, FACIES AND FINGERS

by DEREK WALTON *and* GORDON B. CURRY

ABSTRACT. The possibility of introducing contaminating amino acids while preparing fossils and rocks for analysis is a major problem for molecular palaeontology. The most important source of contamination is human finger tips, which source approximately 100 times the concentration of amino acid than New Zealand fossil shells. Latex gloves can also transmit appreciable quantities of modern day amino acids. However, hierarchical clustering and principal component analysis reveal that the relative proportions of finger-tip amino acids are constant to an extent which allows them to be readily distinguished from those for fossil shells and their enclosing sediment. This approach therefore represents a useful method of checking for contamination by finger tips in analyses of fossil molecules.

AMINO acids are ubiquitous in fossils and rocks, and represent a potentially rich source of information on a wide variety of geological topics (Schroeder and Bada 1976; Curry 1988). For palaeontology, there is considerable potential in studying amino acids from fossil shells and skeletons, for example in the determination of the isotopic composition of individual amino acids which were originally synthesized during the life of the fossil organism. The major problem, however, is that amino acids are so abundant and widely distributed in rocks, sediments and the atmosphere, that there is considerable potential for contamination of fossil shells by diffusion from surrounding sediments and rocks. It is partially with this consideration in mind that attention has recently focused on intracrystalline molecules from brachiopod shells, the rationale being that because such molecules are entombed within, rather than around, biocrystals (Collins *et al.* 1988), they were situated within a protective microenvironment where they were much less prone to contamination. Brachiopods contain a surprising number of different intracrystalline molecules, including various proteins which have recently been sequenced (Curry *et al.* 1991). It is the breakdown products of these proteins (i.e. amino acids and peptides) which offer the best opportunity of recovering genuinely indigeneous molecular information from fossils, and are present in all groups of fossils as far back as the Cambrian (Curry 1988).

However, concentrating on intracrystalline molecules does not completely solve the problem of contamination, because there is still the risk of introducing amino acids during sample preparation. Extraneous amino acids could be added to geological samples during storage (from bacteria, for example) or even by touching specimens with fingers, which are constantly shedding skin composed of vast numbers of amino acids. The question of contamination by finger-tip amino acids was first raised in 1965 (Hamilton 1965; Oró and Skewes 1965), but investigation of this phenomenon has not kept pace with technological advances in amino acid analysis, which have increased incrementally in sensitivity since this early, and often overlooked, work.

It was therefore essential to investigate both the abundance and the relative proportion of finger-tip amino acids as a prelude to a detailed investigation of the molecular palaeontology of fossil shells from New Zealand. It was hoped that identification and an understanding of the characteristics of such amino acids would, when compared with data generated from fossils and sediments using an identical high-sensitivity analysis system, allow the recognition of such contamination and hence eradicate it as a potential distortion of our analyses.

GEOLOGICAL HISTORY OF SAMPLES

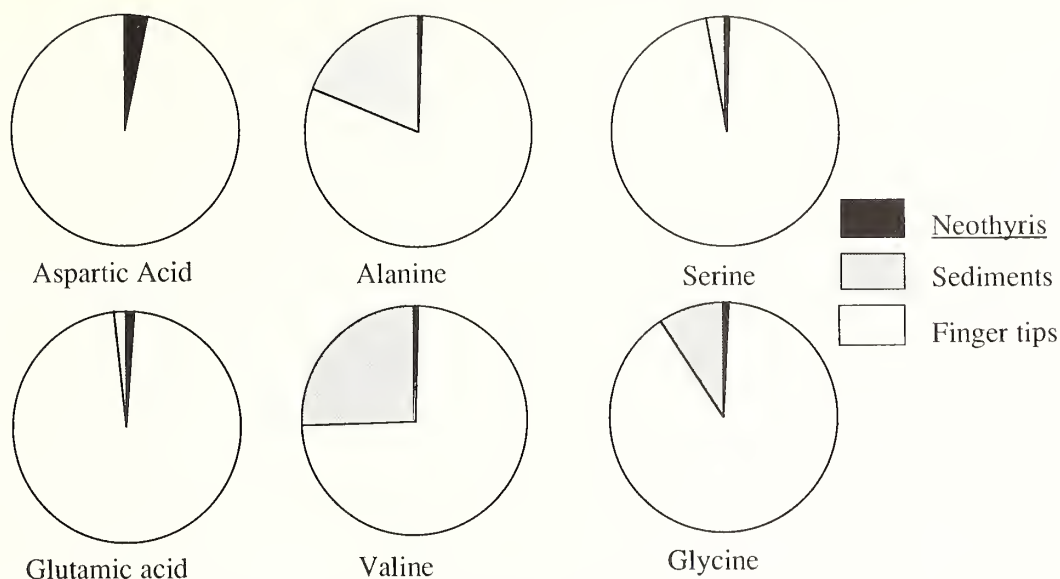
The mid-late Pleistocene sediments and brachiopod fossils investigated were collected from the South Wanganui Basin, which is one of a number of sedimentary basins in the south west of present day North Island, New Zealand. These basins were formed by tectonism related to the subduction of the Pacific Plate below North Island, causing maximum subsidence during the early Miocene. Since this time, there has been general tectonic emergence in these areas (Stern and Davey 1990), indicating that the major control of sedimentation during the mid-late Pleistocene were glacially moderated eustatic changes. Glaciation of South Island began during the Hautawan (*c.* 2.5 Ma) and caused repeated submergence/emergence of the sediments which, coupled with the continuing emergence of the region, resulted in a series of well preserved marine terraces, which have undergone very little burial, along the Taranaki coast (Fleming 1953). It is from these terraces that both the fossils and sediments were collected.

MATERIALS AND METHODS

Free amino acids from finger tips were collected from the fingers of members of the Department of Geology and Applied Geology, University of Glasgow. Sample selection was completely random with respect to the time of day, sex and age of the individuals. Citrate buffer, pH 2.2, was added to the base of a sterile Cel-cult tissue culture plate well (500 μ l of 100 mM), and mixed on a Luckman (Model 802) suspension mixer to ensure complete coverage of the base. The index finger of each individual was wiped with a tissue immediately prior to sampling, to remove traces of solid particles, and then pressed into the well for 15 seconds. Nine samples were taken, including some from fingers which had been washed with either Millipore Reverse Osmosis Water or soap and tap water immediately prior to the test. One well was left untouched to provide a sample blank, and one was touched with the finger in a latex glove that had been used for sample preparation and collection. An aliquot (30 μ l) of each of the samples was applied to the sample frit of the analysis system.

Surface contaminants were removed from a variety of fossil brachiopods by immersion of the shells in an aqueous solution of sodium hypochlorite (10% v/v), and scraping away the encrusting epifauna with a steel needle. Intercrystalline molecules from the powdered or disaggregated shells were destroyed by a second incubation with 10% (v/v) sodium hypochlorite. Amino acids were recovered by decalcifying the shells in an aqueous solution (20% w/v) of EDTA (Ethylenediaminetriacetic acid, disodium salt) at pH 8. EDTA interferes with amino acid analysis, and was therefore removed prior to the analysis of the macromolecular components from the shell by dialysis or ultrafiltration using a 10 kDa cut-off membrane or filter. Amino acids were recovered from sediments by mixing 30 g of dry sediment with 50 ml of ultra-pure water (MilliQ™) in an airtight bottle held at 110 °C for 24 hours. When cool, the liquid was centrifuged (2 k.g.h.), filtered and finally concentrated using a rotary evaporator (Howe Gyrovap).

Hydrolysis of the peptide bonds between amino acids in a polypeptide is a prerequisite of amino acid analysis. Both manual and automatic vapour phase hydrolysis was employed in this study. For manual hydrolysis, 20 μ l of the samples, in newly pyrolysed (500 °C/4 hours) glass hydrolysis tubes, were placed in an airtight flask with 500 μ l of 6 N HCl, and heated to 165 °C for 60 minutes under an Argon blanket (Dupont *et al.* 1989). After hydrolysis the samples were reconstituted in an aqueous solution of EDTA (0.025% w/v; tripotassium salt) and thoroughly mixed. Automated hydrolysis, reproducing these conditions with 6N HCl vapour phase hydrolysis, was performed by the Applied Biosystems 420-H amino acid analyser. An aliquot (10–20 μ l) of solution was loaded onto the amino acid analyser, and derivitized using PITC (Phenylisothiocyanate; Heinrikson and Meredith 1984), prior to identification using a linked narrow bore HPLC (High Performance Liquid Chromatography) system optimized for PTC-amino acids. Amino acids were identified and quantified relative to amino acid standards (Pierce standard H). All analyses were repeated at least once to ensure reproducibility. Water and buffers used were also analysed to check for contamination.



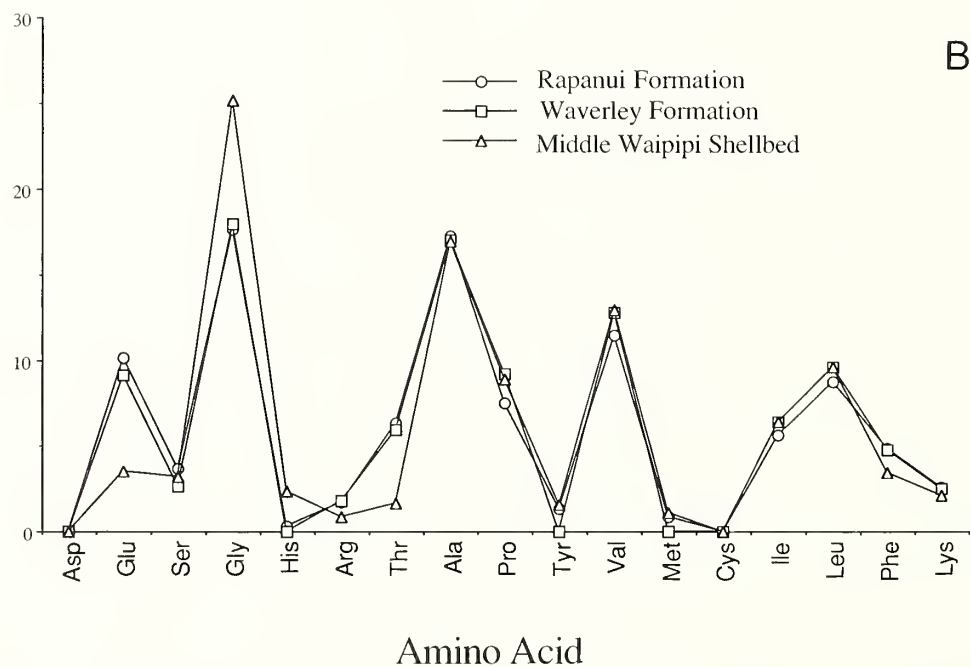
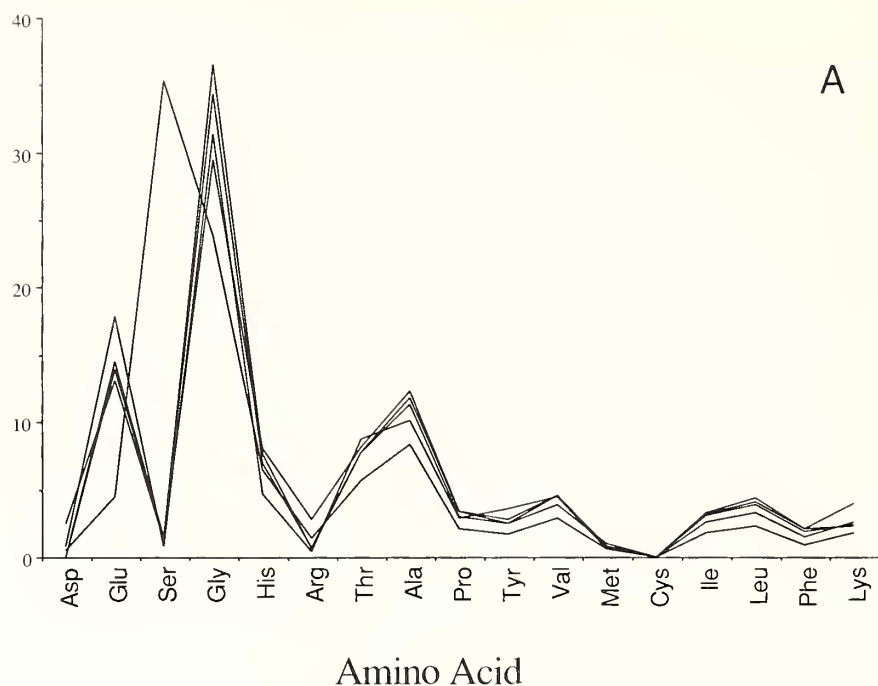
TEXT-FIG. 1. Pie charts showing the absolute proportions of selected amino acids (normalized to nmol/g) from the shells of Plio-Pleistocene *Neothyris* brachiopods, sediments (from the Plio-Pleistocene South Wanganui Basin of New Zealand; see Text-figure 3A for Formation details), and from finger tips (1 ml $\approx$ 1 g).

TABLE 1. Results of amino acid analyses (nmol/g). Figures in brackets refer to sample size.

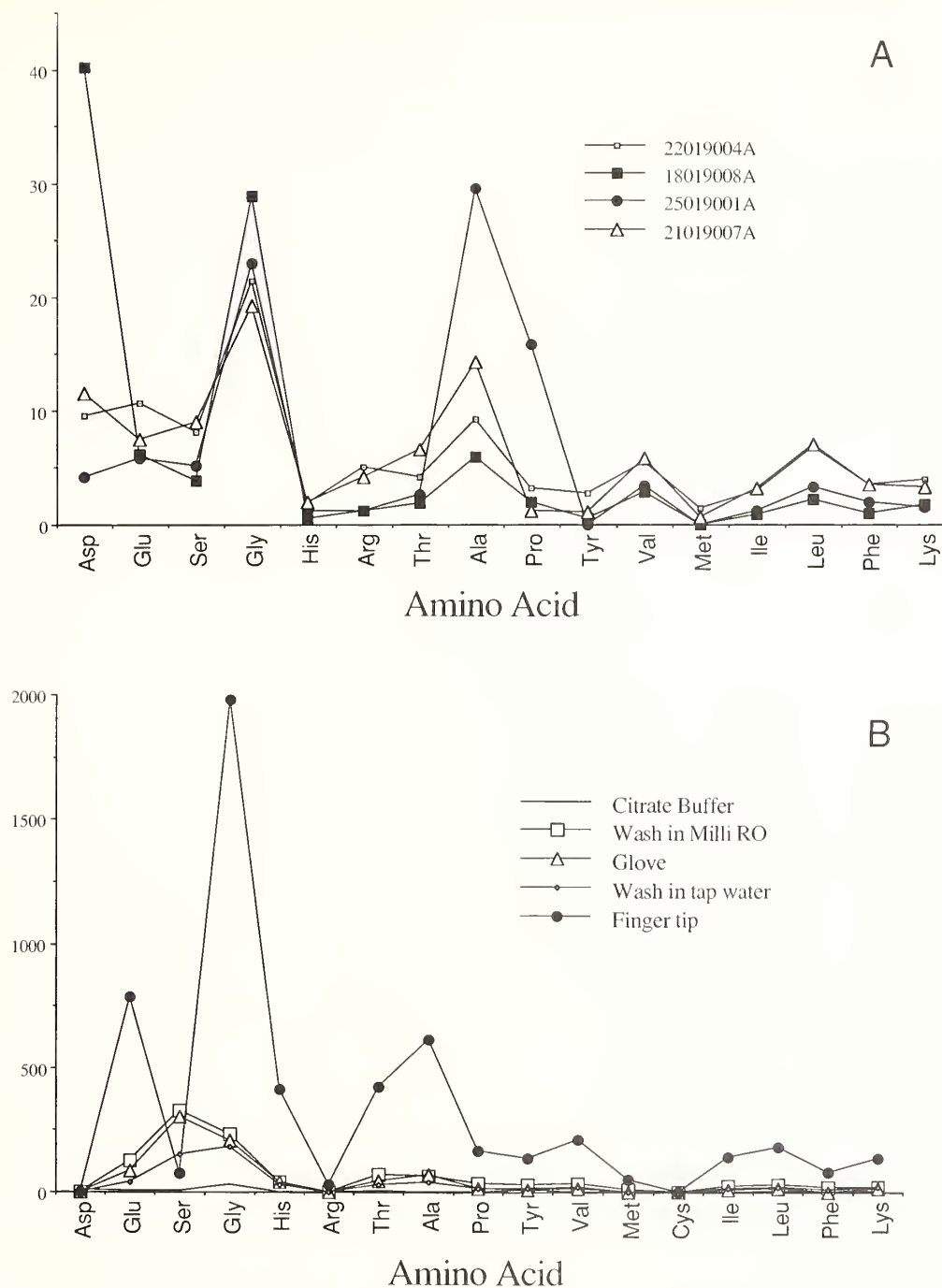
	<i>Neothyris</i> (4)		Finger-tips (8)		Sediments (3)	
	mean	S.D.	mean	S.D.	mean	S.D.
Aspartic acid	0.659	0.450	18.347	15.170	0.000	0.000
Glutamic acid	0.161	0.058	16.020	11.470	0.310	0.197
Serine	0.168	0.089	38.772	44.526	1.091	0.303
Glycine	0.505	0.143	56.211	19.670	5.978	0.768
Alanine	0.211	0.164	22.337	7.383	5.221	1.349
Valine	0.105	0.057	9.323	3.800	3.200	0.910

ABSOLUTE ABUNDANCE OF AMINO ACIDS

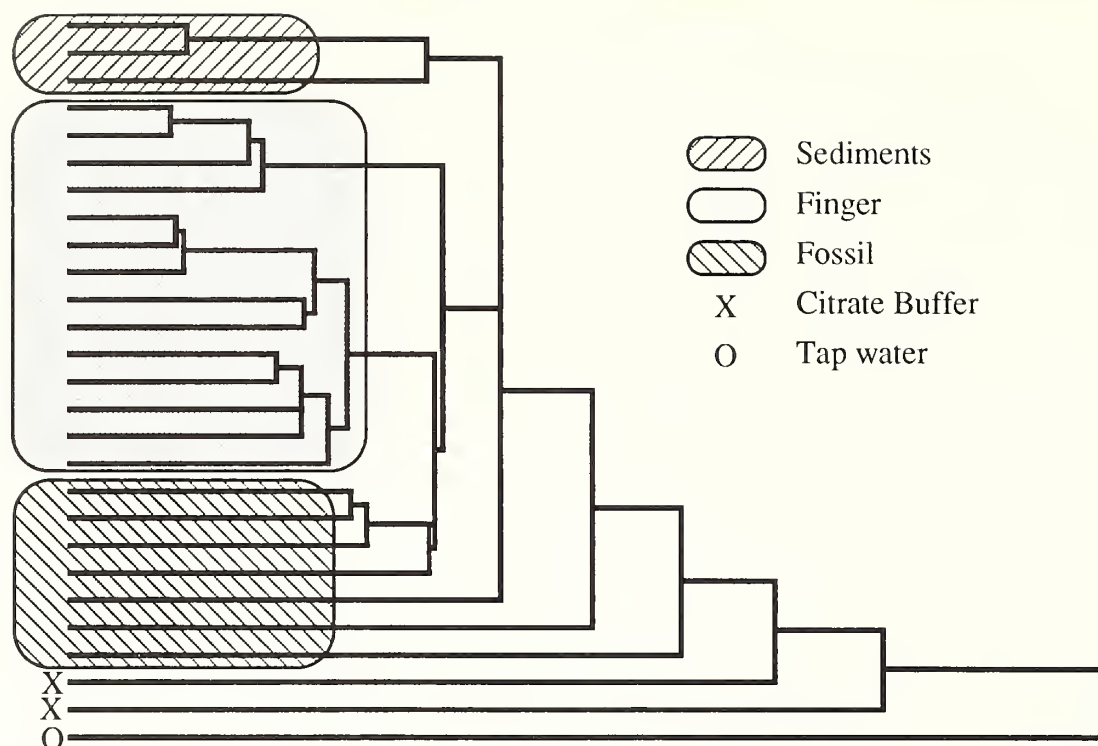
In absence terms, the quantities of amino acids that can be transmitted by finger-tips are considerably greater than those present in fossil shells and in sediments (Table 1; Text-fig. 1). Not surprisingly, there is slight variation in the yields for individual amino acids in some samples, but typically the levels for finger tips are 10 times higher than in sediments, and 100 times higher than in fossils (for example, glycine, see Table 1). Such levels are probably reasonably realistic assessments of the amounts of free amino acids which would be transferred to fossils or sediments by touching them with wet fingers. As the samples were not hydrolysed, amino acids still attached to one another in proteins from the skin would not have been quantified; small fragments of human skin are constantly being shed, and there is no doubt that the potential levels of amino acids transferred by finger contact would be greater than that measured here. Such contamination occurring at a critical stage of sample preparations will clearly overwhelm the indigenous amino acids.



TEXT-FIG. 2. A, relative proportions (Mole %) of the common amino acids from the finger tips of five individuals from the first run of the experiment. B, relative proportion (Mole %) of the common amino acids for New Zealand sediments.



TEXT-FIG. 3. A, relative proportions (Mole %) of the amino acids from the shells of fossil *Neothyris*. Sample 25019001A shows the effect of incomplete removal of EDTA, a phenomenon which provides a check on the preparation purity of the sample. B, absolute properties (un-normalized, the concentrations (pmol) are for amino acids in 30 μ l of buffer) showing the potential levels of contamination from latex gloves in comparison to finger tip data.



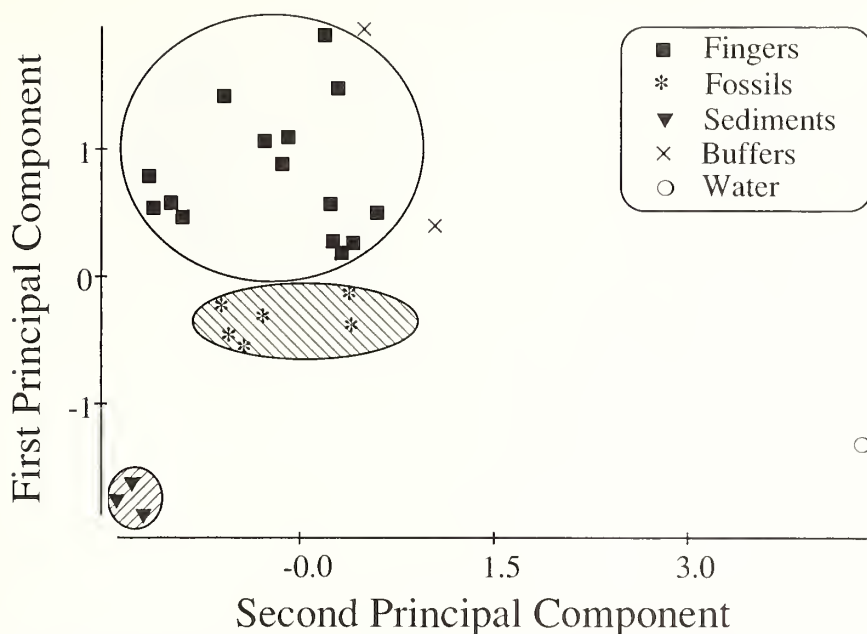
TEXT-FIG. 4. Single linkage cluster analysis (representing nearest neighbour groupings) for the relative proportion data (Mole %), generated by DATADESK™.

RELATIVE ABUNDANCE OF AMINO ACIDS

Amino acid data are often presented in the form of mole percentages which overcomes the difficulty of comparing samples of varying size. Text-figure 2A shows a remarkably consistent pattern in the relative abundance of finger-tip amino acids, with all individuals being rich in either serine or glycine. These results show some similarity with those of Oró and Skewes (1965), where serine is the most common amino acid. In sediments, serine and glycine are also the most abundant (Text-fig. 2B), while glycine is also a major constituent of fossil *Neothyris* shells (Text-fig. 3A). The relative proportions of amino acids are quite consistent within all three groups sampled (Text-figs 2A, 2B and 3A), to the extent that incomplete removal of EDTA from fossil samples becomes readily apparent (Text-fig. 3A). Apart from this sample, the fossil *Neothyris* all have consistent amino acid profiles.

Superficially there are a number of common features between these three datasets, but such subjective assessments are potentially misleading. To produce a more rigorous assessment of the relative similarity between samples, hierarchical clustering analysis using the statistical programme DATADESK™ on a Macintosh micro-computer was applied to the relative abundance data. The resulting cluster diagram resolves the finger tip, sediment and fossil shell amino acid data into discrete clusters (Text-fig. 4). The citrate buffer and tap water have been included as outgroups.

Principal component analysis (PCA) using DATADESK™ was also applied to the datasets (Text-fig. 5), and this confirms the groupings of the cluster plot. A useful attribute of PCA is that it is possible to use the eigen-vector values to determine which elements (in this case individual amino acids) are most important in distinguishing between the different groups. Text-figure 5 shows



TEXT-FIG. 5. Scatter plot of the first two principal components for relative proportion data (Mole %), generated by DATADESK™. These data do not take into account variations in the actual concentrations of the amino acids.

that the clear resolution between sediments, fossils, and fingers is achieved along the first principal component axis, which is aligned in the direction of maximum variability and in this case contributes 26.9% of the total variation detected. Examining the eigen-vector values from this analysis, it is clear that this differentiation primarily reflects high scores for serine (+0.273), histidine (+0.276), arginine (−0.258), proline (−0.275), tyrosine (+0.229), valine (−0.377), methionine (−0.205), isoleucine (−0.323), leucine (−0.347) and phenylalanine (−0.345). The sign of these scores is also informative, indicating that samples which have high scores on this eigen-vector (i.e. the fingers) contain large amounts of serine, histidine and tyrosine, and relatively low yields of arginine, proline, valine, methionine, isoleucine, leucine and phenylalanine.

DISCUSSION

In one respect it is not surprising to discover a clear differentiation between these three groups of samples. Finger-tip amino acids are predominantly derived from human skin proteins. Amino acids from sediments presumably come from a complex mixture of sources including the breakdown of various life-forms which originally lived in or on the sediment and mobile amino acids carried in by percolating ground waters. The fossil amino acids considered here have been extracted from intracrystalline macromolecules; most published data from shells have also included a component of intercrystalline macromolecules (e.g. Jope 1967a, 1967b; Weiner *et al.* 1976), which are not protected by shell crystallites, and hence may be easily degraded or contaminated. It is very encouraging for the study of amino acids in these New Zealand successions that the finger-tip data can be so readily distinguished from the fossil and sediment data, both in terms of absolute abundance and mole percentages. Further samples of fossil shells have been analysed, and a similar pattern of differentiation from finger-tip and sediment data is apparent.

In practical terms, the use of clustering and statistical approaches represents an important and

rapid method of checking for human contamination in geological samples. As the absolute abundance of finger-tip amino acids is so much greater than that of fossils, any contamination should produce an analysis which clusters with the former rather than the latter, and this is probably also true for sediments although to a lesser extent.

The results of this investigation have also provided important information for sample preparation. High levels of contamination from finger-tip amino acids are to be expected, but these experiments have shown that even hands which have washed prior to handling samples could be a significant source of contamination. Much more surprising, and potentially worrying, is the discovery that even latex laboratory gloves can be a source of contamination amino acids (Text-fig. 3B). Latex gloves are widely used in laboratories, but obviously they give a false sense of security with modern high-sensitivity amino acid analysers capable of detecting a few picomoles (10^{-12} mole) of each amino acid. For optimum recovery of uncontaminated indigenous amino acids from fossils and sediments, it is necessary to minimize or completely eradicate any handling of the sample or of the interior surfaces of any vessel involved in the release of the incarcerated amino acids.

Acknowledgements. We thank Dr M. Cusack for her comments on this paper, and the members of the Department of Geology and Applied Geology for providing samples. A UK NERC studentship to D.W. (GT4/89/GS/42), and funding from the Royal Society and NERC to G.B.C. are gratefully acknowledged.

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BAJOCIAN STEPHANOCERATID AMMONITES FROM THE BAKONY MOUNTAINS, HUNGARY

by A. GALÁ CZ

ABSTRACT. Ammonites are described from the Bajocian *Otoites sauzei* and *Stephanoceras humphriesianum* Zones in a stratigraphically discontinuous red, pelagic limestone sequence. The fauna consists mainly of phylloceratids and lytoceratids, thus showing a typical Mediterranean association. The Ammonitina are almost exclusively represented by stephanoceratids, suggesting a part of the *Sauzei* Zone and two subzones of the *Humphriesianum* Zone. The *Sauzei* Zone is indicated by a single specimen of *Emileia* sp. The upper part of the *Stephanoceras humphriesianum* Subzone is suggested by *Dorsetensia subsecta* Buckman and associated stephanoceratids: *Stephanoceras triplex* Weisert, *S. scalare* Weisert, *S. mutabile* (Quenstedt), and *S. leoniae* Schmidtil and Krumbeck, while the basal part of the *Teloceras blagdeni* Subzone is identified from an assemblage of *Stephanoceras sturani* Pavia, *S. (Normannites) orbigny* Buckman and *S. (N.)* sp. aff. *fortis* Pavia. The stratigraphic representation in the sequence is rather incomplete. However, a description of its fauna may help to evaluate similar assemblages recorded in other areas of the Mediterranean region.

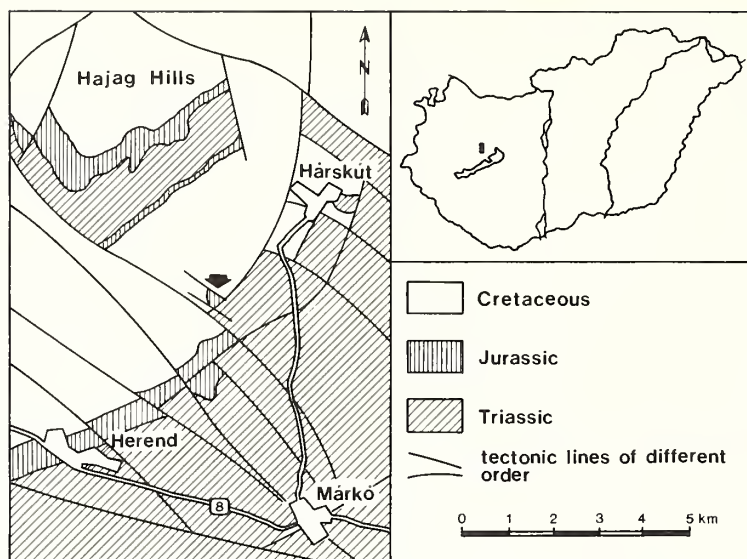
DETAILED studies on Jurassic ammonites from the Bakony Mountains (Transdanubian Hungary) have resulted in the recognition of exceptionally rich Liassic faunas. These results contributed substantially to our understanding of Mediterranean Lower Jurassic stratigraphy. Recent investigations indicate a similar, important role for the Middle Jurassic faunas. The ammonites described here came from a typical Mediterranean Jurassic section of red, nodular pelagic limestones below an ammonite-free radiolarite. The fauna represents only a small part of the Middle Jurassic Bajocian stage and consists mainly of phylloceratids and lytoceratids; the Ammonitina are overwhelmingly represented by stephanoceratids.

Stephanoceratidae, that characteristic Bajocian group, are very incompletely known, especially in the Mediterranean. In spite of the relatively large number of described species, the interpretation of taxa and their stratigraphic distribution is far from clear. The aim of this paper is to make known the taxonomy and stratigraphic occurrences of some stephanoceratids within a small, but stratigraphically well-defined succession.

LOCALITY AND SUCCESSION

Közöskút Ravine is a narrow valley at the southwestern margin of the Hajag Hills, near the village of Hárskút, in the Bakony Mountains (Text-fig. 1). The Jurassic sequence exposed here was first mentioned by Noszky (1943), who gave a short description of the local stratigraphy. The Hettangian Dachsteinkalk-type limestone is overlain by higher Lower Liassic, then Toarcian and Bajocian ammonitic limestones, which are followed by a cherty radiolarite, then a complete Upper Jurassic-Lower Cretaceous calcareous succession. Later, in a comprehensive treatment of the Jurassic of Hungary, Noszky (1961) gave a similar summary, indicating some non-sequences in the section.

The outcrop was visited during the Mediterranean Jurassic Colloquium in 1969. A detailed description and sections outlining the Jurassic sequence was given by Fülöp *et al.* (1969, fig. 19) and Fülöp (1971, fig. 10). Konda (1970, pp. 192–193) has described the lithology and the microfacies features of the Liassic and Middle Jurassic rocks. The biostratigraphic evaluation of the ammonite faunas collected was made by Géczy (1971, 1976) for the Liassic, and a preliminary account of the results of Middle Jurassic studies has also been published (Galácz 1976).



TEXT-FIG. 1. Location of Közöskút Ravine in the Bakony Mountains, Transdanubian Hungary.

These biostratigraphic evaluations made it clear that considerable hiatuses can be identified within this sequence with a basically uniform lithology. The Liassic and the Bajocian is represented here by the typical Mediterranean Rosso Ammonitico limestone, which is a thin, pelagic, nodular carbonate with ferromanganese nodules and crusts. These sequences are common in the Bakony Mountains and elsewhere in the Mediterranean region, and are generally regarded as accumulations on elevated parts of submarine topographic highs in the Jurassic deep-sea Tethys.

In the Közöskút sequence, the incomplete representation of the Liassic and Middle Jurassic is demonstrated by the complete lack of the Sinemurian and Aalenian stages (see Text-fig. 2). However, the documented stages are only partially represented, for the 119 cm thick Lower Jurassic limestones yielded ammonites merely from the *Tragophylloceras ibex* Zone of the Pliensbachian and the *Hildoceras bifrons* and *Dumortieria levesquei* Zones of the Toarcian. Similarly, the 133 cm thick Bajocian series is represented only by the *Otoites sauzei* and the *Stephanoceras humphriesianum* Zones.

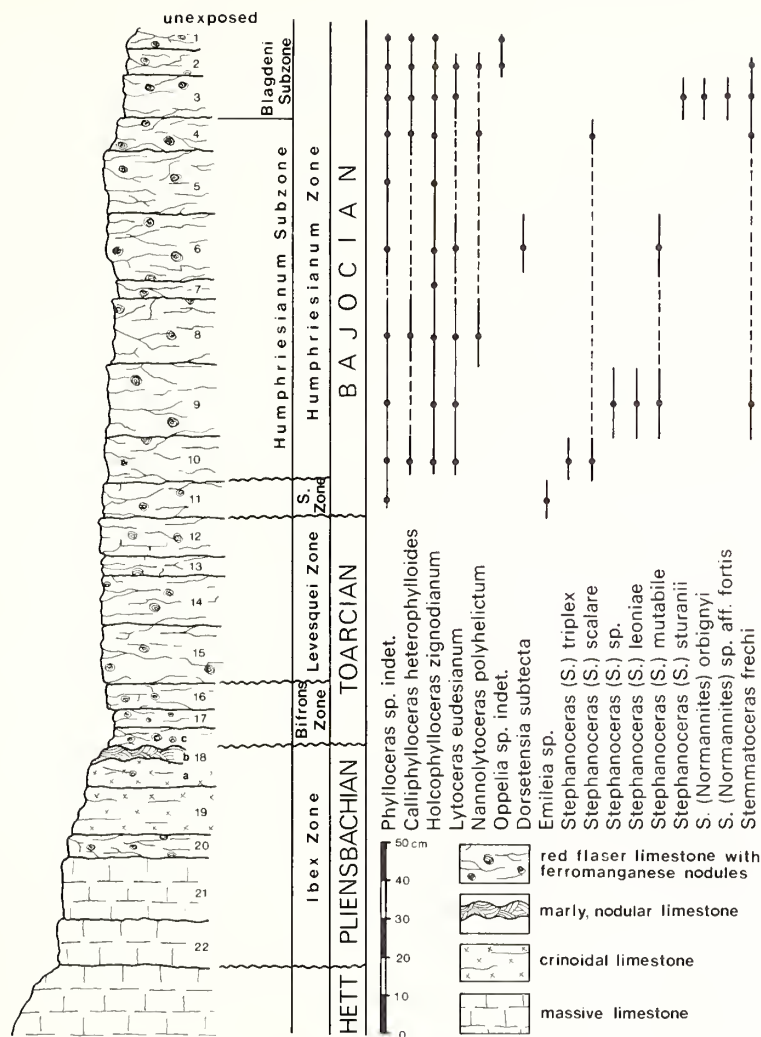
Detailed stratigraphic evaluation of the Bajocian ammonites revealed the presence of further, minor discontinuities. Bed 11, with a single *Sauzei* Zone ammonite species and only two specimens, certainly represents only a portion of this zone. The limestone above Bed 11 gave a fauna with a very rich *Stephanoceras* association, which can be correlated to a limited extent with the middle and upper parts of the *Humphriesianum* Zone.

Jurassic successions of similar lithology and discontinuous biostratigraphic representation, where the paracomformable beds contain only a few faunal horizons of certain stages, are common in the Mediterranean pelagic realm. Thus descriptions of locally intermittent faunal sequences may help to piece together a reliable picture of the ammonite successions for the wider area.

COMPOSITION AND CORRELATION OF THE BAJOCIAN FAUNA

Bed 11, the single layer of *Otoites sauzei* Zone age, gave only two ammonite specimens; therefore, detailed evaluations were made only for the overlying ten beds belonging to the *Stephanoceras humphriesianum* Zone.

In general aspect the fauna is typically pelagic. The megafauna is almost entirely represented by

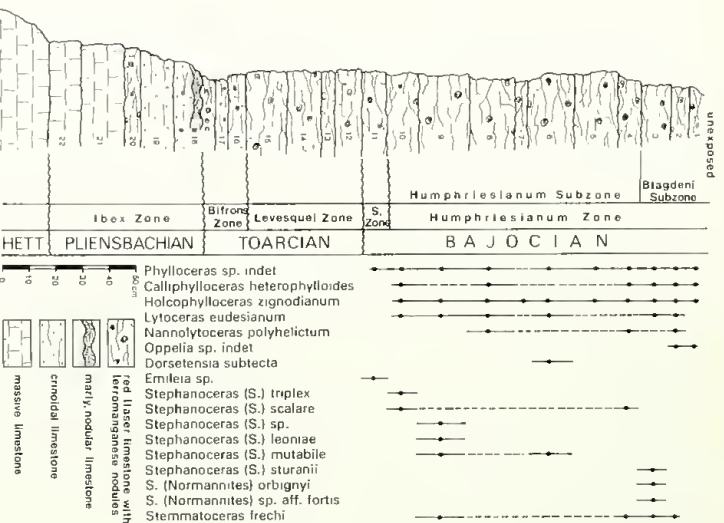


TEXT-FIG. 2. The Lower and Middle Jurassic limestone sequence in the Kőzőskút Ravine, with the range of the Bajocian ammonites (S. = Sauzei).

ammonites: only a few belemnite rostra, a single bivalve (*Inoceramus* sp.), and one nautiloid were collected. Benthonic elements are completely missing.

The composition of the ammonite assemblages is characteristically Mediterranean, with phylloceratids dominant and lytoceratids common. The percentage distribution of the ammonite fauna gave the following values by suborders: Phylloceratina = 54%; Lytoceratina = 13%; Ammonitina = 33%. A closer analysis of the Ammonitina reveals that this is an almost pure stephanoceratid fauna: there are eighty-seven *Stephanoceras*, *Normannites* and *Stenmatoceras* specimens, but only three poorly preserved oppeliids and a single *Dorsetensia*. Other groups (e.g. sphaeroceratids: *Chondroceras*, *Sphaeroceras*; haploceratids: *Strigoceras*, *Cadomoceras*, *Poecilomorphus*) are conspicuous by their absence.

These features make the Kőzőskút fauna exceptional among assemblages of similar age. The recently monographed Sub-Mediterranean faunas from Digne, SE France (Pavia 1983), from the



TEXT-FIG. 2. The Lower and Middle Jurassic limestone sequence in the Kőzöskút Ravine, with the range of the Bajocian ammonites (S. = Sauze).

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These features make the Kőzöskút fauna exceptional among assemblages of similar age. The recently monographed Sub-Mediterranean faunas from Digne, SE France (Pavia 1983), from the

Betic Cordilleras (Sandoval 1983) and from the Iberian Cordilleras (Fernandez López 1985) are similar in having common elements, but different in faunal composition. The only places where similar faunas were recorded (but only partially documented) are within the s.s. Mediterranean region: from the Alpi Feltrine, N. Italy (Della Bruna and Martire 1985) and from the Appennino marchigiano, Central Italy (Cecca *et al.* 1986).

In the absence of non-stephanoeceratid Ammonitina, a correlation with other *Humphriesianum* Zone faunas is difficult. A further complication is that the subzonal subdivision of the *Stephanoceras humphriesianum* Zone, as well as its successive faunal horizons, are incompletely known. Parsons (1976) gave a comprehensive overview of the subzonal units, but in the last decade important new results have been published. Some of the recently suggested subzonal divisions are given in Table 1. This shows that the infrazonal units of the Bajocian *Humphriesianum* Zone are far from generally agreed. While a subdivision into three or four subzones seems to be accepted, several 'horizons' are suggested without exact inter-regional correlation.

PARSONS 1976 (adopted here)	PAVIA 1983	SANDOVAL 1983	DIETL, HAGER and SAUER 1984	FERNANDEZ LÓPEZ 1985	OHMERT 1988
Subfurcatum Zone	Niortense Zone	Leptosfincntes Zone	Niortense Zone	Subfurcatum Zone	Niortense Zone
Humphriesianum Zone Blagdeni Subzone	Humphriesianum Zone Blagdeni Subz. Dubium Hor.	Humphriesianum Zone Blagdeni Subzone	Humphriesianum Zone Blagdeni Subzone	Humphriesianum Zone Blagdeni Biohorizon	Humphriesianum Zone Blagdeni Subzone
Humphriesianum Zone Humphriesianum Subzone	Humphriesianum Zone Humphriesianum Subzone	Humphriesianum Zone Humphriesianum Subzone	Humphriesianum Zone Humphriesianum Subzone	Humphriesianum Zone Scalare Biohorizon	Humphriesianum Zone Humphriesianum Subz. Umbilicum Horizon
Humphriesianum Zone Romani Subzone	Humphriesianum Zone Romani Subz. Paululus H. Edouardiana H.	Humphriesianum Zone Cycloides Subzone	Humphriesianum Zone Pinguis Subzone	Humphriesianum Zone Nodosum Biohorizon	Humphriesianum Zone Romani Subzone
Sauzei Zone	Sauzei Zone	Sauzei Zone	Sauzei Zone	Sauzei Zone	Sauzei Zone

TABLE 1. Comparison of some recent subdivisionings of the Bajocian *Stephanoceras humphriesianum* Zone.

The *Humphriesianum* Zone fauna of the Kőzőskút Ravine can be divided into two assemblages. The lower one, from Bed 10 to Bed 4 contains stephanoceratids, *Stephanoceras triplex*, *S. scalare*, *S. mutabile*, *S. leoniae*, and the associated *Dorsetensia subsecta*. The best match with this fauna is that from Beds 355 to 339 of the Chaudon section, Digne area (Pavia 1983, Table IIIb). While some of Pavia's determinations are reinterpreted here (see descriptions below), the basic composition of stephanoceratids s.s. is very similar. Thus the lower seven beds of the Kőzőskút *Humphriesianum* Zone section can be correlated with the upper part of the *Stephanoceras humphriesianum* Subzone.

In Bed 3 new elements appear: *Stephanoceras sturani* and *Normannites* spp. (see Text-fig. 2). Comparable forms are known from the Digne area in the basal part of the *Blagdeni* Subzone ('*Dubium* horizon' of Pavia 1983, pp. 36–37). Accordingly, the topmost part of the Kőzőskút Bajocian belongs to the lower *Blagdeni* Subzone, and the whole sequence encompasses the boundary beds of the two higher subzones of the *Humphriesianum* Zone.

SYSTEMATIC PALAEONTOLOGY

Deposition of specimens. All the ammonites studied are deposited in the Palaeontological Collections of the Hungarian Geological Survey, Budapest. Measured and illustrated specimens have inventory numbers.

Dimensions. Measurements are given in millimetres, in the following order and with the following abbreviations: maximal preserved diameter (MDm); diameter (Dm); whorl height (Wh); whorl breadth (Wb); and umbilical diameter (Ud). Numbers in parentheses refer to dimensions as a

percentage of the diameter. Pr indicates number of primary ribs, S the number of secondary ribs per whorl.

Order AMMONOIDEA Zittel, 1884
 Suborder PHYLLOCERATINA Arkell, 1950
 Superfamily PHYLLOCERATACEAE Zittel, 1884
 Family PHYLLOCERATIDAE Zittel, 1884
 Genus CALLIPHYLLOCERAS Spath, 1927

Type species. Phylloceras disputabile (Zittel, 1868) = *Ammonites tatricus* Kudernatsch *non* Pusch, 1852, p. 4, pl. 1, figs 1–4, by original designation of Spath (1927–33, p. 24).

Calliphyloceras heterophylloides (Oppel, 1856)

Plate 1, fig. 4; Text-fig. 3A

- 1856 *Ammonites heterophylloides* Oppel, p. 493.
 v 1871 *Phylloceras heterophylloides* Oppel; Neumayr, p. 331, pl. 15, fig. 1a–c.
 v 1878 *Phylloceras heterophylloides* Oppel; Bayle, pl. 32, figs 1, 2, 5–8.
 1927 *Phylloceras* gr. de *heterophylloides* Oppel; Roman and Pétouraud, p. 16, pl. 2, figs 9 and 10.
 non 1937 *Phylloceras* aff. *heterophylloides* Oppel; Kakhadze, p. 126, pl. 1, fig. 4.
 ?1937 *Phylloceras heterophylloides* Oppel; Horwitz, p. 240, pl. 9, fig. 1.
 1956 *Calliphyloceras heterophylloides* Oppel; Kakhadze and Zesashvili, p. 18, pl. 2, figs 2 and 3.
 ?1973 *Calliphyloceras* cf. *heterophylloides* (Oppel); Myczinsky, p. 59, pl. 1, fig. 6.
 1976 *Calliphyloceras heterophylloides* (Oppel); Joly, p. 213, and figures.

Material. Eleven measured, well preserved internal moulds and several fragments or strongly corroded specimens.

Measurements.

	MDm	Dm	Wh	Wb	Ud
J9471	94.5	94.5	54.5 (57.5)	36 (38)	6 (6.5)
		74	42 (56.5)	25 (33.5)	5.5 (7.5)
		67.5	38 (56)	24 (35.5)	4.5 (6.5)
		41.5	23 (55)	13.5 (32.5)	4 (10)
		21	10 (47)	7 (33)	4 (19)
		11	5 (45)	4.5 (41)	2.5 (22)
J9477	70.5	70.5	41 (58)	24 (34)	5 (7)
		51	29 (57)	18 (35)	4 (8)

Description. Medium size ammonite. Most of the studied specimens are well preserved internal moulds, but the body chamber is usually missing. The umbilicus is narrow, attaining only 5–7% on the outer whorls. The whorl section is high-oval with steep umbilical wall, broadly arched, slightly compressed flanks and narrow, highly arched venter. The inner whorls are inflated. The whorls are smooth, shell-sculpture cannot be seen. The larger forms show seven, rarely eight constrictions per whorl. The constructions are slightly prorsiradiate and straight, becoming curved near the venter, which they cross with a strong forward arch.

The suture line (Text-fig. 3A) is of characteristic *Phylloceras* type, with diphyllid first lateral saddle, triphyllid second lateral saddle, and diphyllid then monophyllid auxiliary elements.

Remarks. The lectotype was designated by Joly (1976, p. 213, pl. 21, fig. 1). This is a relatively large, wholly septate specimen with partially preserved shell from the Upper Bajocian of St Vigor, Calvados, France. Joly figures (1976, pl. 21, fig. 3) another specimen from the same locality as 'paratype'. This is the original of plate 42, figure 2 of Bayle (1878), and thus should be regarded as a topotype. The Közöskút specimens are readily comparable with those from St Vigor. The single difference is in the umbilical width which is extremely small in the large lectotype. On the basis of the detailed statistical studies of Joly (1976, pp. 215–223), *C. heterophylloides* can be easily

distinguished from the similar, but somewhat younger (i.e. uppermost Bajocian to Callovian), *C. disputabile* (Zittel).

Distribution. The exact horizon of the type within the Upper Bajocian is uncertain. The literature mentions this species usually from the *Humphriesianum* Zone, whereas the Madagascan material of Joly came from the Upper Bathonian.

C. heterophylloides is one of the commonest species in the Közöskút Bajocian, occurring in almost every bed of the *Humphriesianum* Zone.

Genus *HOLCOPHYLLOCERAS* Spath, 1927

Type species. *Ammonites zignodianus* (d'Orbigny, 1848, p. 493, pl. 182), see Galácz 1980, p. 41.

Holcophylloceras zignodianum (d'Orbigny, 1848)

Plate 2, fig. 2; Text-fig. 3C

- 1848 *Ammonites Zignodianus* d'Orbigny, p. 493, pl. 182, figs 1–3.
 v 1871 *Phylloceras mediterraneum* Neumayr, p. 340, pl. 17, figs 2–5.
 1980 *Holcophylloceras zignodianum* (d'Orbigny); Galácz, p. 41, pl. 5, figs 4 and 5; pl. 6, fig. 1; pl. 7, fig. 1; text-figs 30–32. (*cum syn.*).

Material. Twenty-five specimens in various states of preservation.

Measurements.

	Mdm	Dm	Wh	Wb	Ud
J9468	92	92	50 (52.5)	34 (37)	12 (13)
		68.5	35 (51)	23 (33.5)	10 (14.5)

Description. Medium to large specimens; the figured specimen (J9468) is a well preserved internal mould. The deep and narrow umbilicus has low, vertical walls, which form distinct shoulders with the slightly convex flank. The venter is narrow and highly arched. The whorls are smooth, except for the characteristic constrictions, which are prorsiradial furrows with a sharp break just above the middle of the flanks. There are seven constrictions per whorl. The figured specimen shows the end of the phragmocone at 95 mm diameter; no specimen with an entire body chamber and aperture was found.

The suture line (Text-fig. 3C) shows diphyllid first lateral and triphyllid second lateral saddle and deep lobes.

Remarks. This species was discussed in detail recently (Galácz 1980, pp. 41–44), so this short reference to newly collected specimens seems sufficient.

Distribution. *H. zignodianum* is a species of extremely wide stratigraphic range, appearing in the Bajocian *Otoites sauzei* Zone and enduring up to the Upper Jurassic. In the Közöskút sequence this is the commonest ammonite, occurring in almost every bed of the *Humphriesianum* Zone.

EXPLANATION OF PLATE I

- Fig. 1. *Emileia* sp. indet. J9469; Közöskút; Bed 11, *Otoites sauzei* Zone; lateral view, $\times 1$.
 Fig. 2. *Stephanoceras* (*Stephanoceras*) *mutabile* (Quenstedt). J9496; Közöskút; Bed 9, *Stephanoceras humphriesianum* Subzone; lateral view, $\times 1$.
 Fig. 3. *Stephanoceras* (*Stephanoceras*) sp. J9488; Közöskút; Bed 9, *Stephanoceras humphriesianum* Subzone; lateral view, $\times 0.6$.
 Fig. 4. *Calliphyllloceras heterophylloides* (Oppel). J9477, Közöskút; Bed 2, *Teloceras blagdeni* Subzone; lateral view, $\times 0.75$.
 Fig. 5. *Stephanoceras* (*Stephanoceras*) *sturanii* Pavia. J9461; Közöskút; Bed 3, *Teloceras blagdeni* Subzone; lateral view of a specimen with distorted body chamber, $\times 1$.



GALÁ CZ, *Emileia*, *Stephanoceras*, *Calliphylloceras*

Suborder LYTOCERATINA Hyatt, 1889
 Superfamily LYTOCERATACEAE Neumayr, 1875
 Family LYTOCERATIDAE Neumayr, 1875
 Genus NANNOLYTOCERAS Buckman, 1905

Type species. *Ammonites pygmaeus* (d'Orbigny 1842–51, p. 391, pl. 129, figs 12 and 13), by original designation of Buckman (1905, p. 151).

Nannolytoceras polyhelicum (Böckh, 1881)

Plate 3, fig. 2

- v 1881 *Lytoceras polyhelicum* Böckh, p. 35, pl. 1, figs 2 and 3.
 1964 *Eurystomiceras polyhelicum* (Böckh); Pugin, p. 42, pl. 3, fig. 7; text-fig. 8 (*cum syn.*).
 1980 *Nannolytoceras polyhelicum* (Böckh); Galácz, p. 51, pl. 10, fig. 2; pl. 11, fig. 1; text-figs 39–41 (*cum syn.*).

Material. Four poorly preserved, fragmentary internal moulds.

Measurements.

	MDm	Dm	Wh		Wb		Ud
J9476	61	61	18 (29.5)		18 (29.5)		29 (47.5)
J9475	54	54	15 (28)		15 (28)		26.5 (49)
		41	13.5 (33)		13.5 (33)		19.5 (47.5)

Description. The figured specimen is a small fragment. The umbilicus is wide, the whorl section high-oval, becoming subcircular on the body chamber. The umbilical wall and the flanks are rounded, the venter is slightly arched. The whorls are smooth, only constrictions are present. The number of constrictions is five on the outermost whorl. They are projected and slightly curved, crossing the venter perpendicularly. The frontal margin of the constrictions is inflated. No entire body chamber is preserved, thus the aperture cannot be seen. Suture line is not visible.

Remarks. This species was discussed (Galácz 1980, p. 51) on the basis of bigger and better preserved material. The Kőzőskút specimens match these previously studied forms well.

Distribution. The type (Böckh 1881, pl. 1, fig. 1) came from the *Niortense* Zone of the Mecsek Mountains, southern Hungary, but from there and elsewhere, *Humphriesianum* Zone occurrences were also mentioned. The specimens described here came from Beds 8, 4 and 2, i.e. from the middle to the upper part of the *Humphriesianum* Zone.

Suborder AMMONITINA Hyatt, 1889
 Superfamily HILDOCERATACEAE Hyatt, 1867
 Family SONNINIIDAE Buckman, 1892
 Genus DORSETENSIA Buckman, 1892

Type species. *Ammonites Edouardianus* (d'Orbigny 1844, p. 392, pl. 130, figs 3–5), by original designation of Buckman (1892 p. 302).

Dorsetensia subsecta Buckman, 1892

Plate 2, fig. 4; Text-fig. 3B

- v 1892 *Dorsetensia subsecta* Buckman, p. 309, pl. 54, figs 3–5; pl. 55, figs 1 and 2.
 p. 1935 *Dorsetensia subsecta* Buckman; Dorn, p. 103, pl. 21, fig. 2; pl. 25, fig. 7; pl. 29, fig. 4; pl. 8, figs 9 and 10 only.
 ?1937 *Witchellia* (*Dorsetensia*) *subsecta* Buckman; Horwitz, p. 254, pl. 10, fig. 4.
 ?1937 *Witchellia subsecta* Buckman; Gillet, p. 67, text-fig. 49.
 1943 *Dorsetensia subsecta* Buckman; Roché, p. 13, pl. 2, fig. 2.

- 1949 *Dorsetensia Thilense* Maubeuge, p. 172, pl. 12; text-figs on p. 172.
 1951 *Dorsetensia subsecta* Buckman; Maubeuge, p. 34, pl. 12, fig. 2.
 1951 *Dorsetensia* cf. *subsecta* Buckman; Maubeuge, p. 36, pl. 10, fig. 3.
 ?1961 *Dorsetensia* sp. aff. *thilense* Maubeuge, p. 71, fig. on p. 72.
 1967 *Dorsetensia subsecta* Buckman; Kopik, p. 27, pl. 7, fig. 5; pl. 8, figs 1 and 2; pl. 9, fig. 1; text-figs 13 and 14.
 1968 *Dorsetensia liostraca subsecta* Buckman; Huf, p. 103, pls 41–47.
 non 1973 *Dorsetensia* cf. *D. subsecta* [sic!] Buckman; Imlay, p. 71, pl. 28, figs 1–7; pl. 29, fig. 7.
 1977 *Dorsetensia* cf. *subsecta* Buckman; Parsons, p. 212, pl. 13, fig. 1.
 1983 *Dorsetensia* (*Dorsetensia*) *subsecta* Buckman; Pavia, p. 61, pl. 5, figs 3 and 8.
 ?1984 *Dorsetensia subsecta* Buckman; Dietl, Franz and Reis, p. 310, text-fig. 2/1.
 1985 *Dorsetensia subsecta* Buckman; Schlegelmilch, p. 66, pl. 20, fig. 3.

Material. A single, well preserved, but partly fragmentary internal mould.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Wh/Wb
J9494	210	210	88 (42)	38 (18)	52 (25)	2·31
		156	70·5 (45)	31 (20)	36 (23)	2·27

Description. A large specimen with a relatively wide, shallow umbilicus. The whorl section is high, compressed. The umbilical wall is flat, oblique, forming a distinct shoulder with the flank. The lateral side is slightly convex, and forms a ventro-lateral edge with the narrow, tectiform venter. The internal mould bears a blunt ventral keel showing traces of the hollow keel of the shell. The preserved parts of the inner whorls have no traces of ribbing. The specimen is septate up to 150 mm diameter, and has preserved body chamber of nearly half a whorl. The terminal part of the last whorl, with the aperture, is missing.

The suture line is partially visible (Text-fig 3B). This shows finely serrated lobes and saddles as compared to those usual in the genus. However, the broad lateral lobe indicates the characteristic *Dorsetensia*-type suture.

Remarks. *D. subsecta* is distinguished from the similar, large *Dorsetensia* by its relatively wide umbilicus and high, flattened, nearly parallel flanks. Huf (1968, p. 103) gave a detailed discussion on the variations. The whole group, with its size, style of ornament on the early whorls and septecarinate venter shows affinities to Sonniniinae, and may be better placed in the genus *Sonninites* Buckman (J. Callomon, pers. comm. 1986).

The Kőzőskút specimen is very similar to the large forms described by Maubeuge (1951, p. 34), the closest form being the variety previously designated as *D. thilense* (Maubeuge 1949, p. 172). Another very similar form is that described by Hoyer mann (1917, p. 39) and refigured later by Huf (1968, pl. 43, fig. 1c; pl. 44, fig. 1).

Distribution. *D. subsecta*, like other large *Dorsetensia* species, usually occurs in the lower part of the *Humphriesianum* Zone. In the type area of Osborne, Dorset, Parsons (1976, pp. 121, 131) collected topotypes in association with typical *Romani* Subzone ammonites. Higher occurrences within the *Humphriesianum* Zone are also known (see e.g. Pavia 1983, p. 61). The Kőzőskút specimen came from Bed 6, i.e. from the higher part of the *Humphriesianum* Subzone.

Superfamily STEPHANOCERATAEAE Neumayr, 1875

Family OTOITIDAE Mascke, 1907

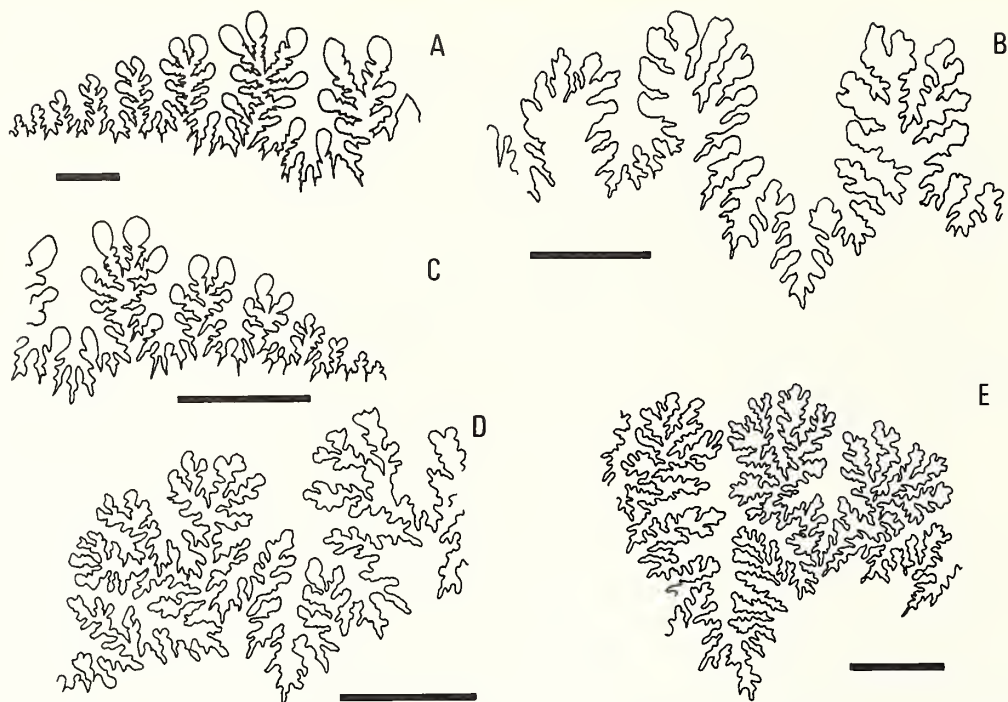
Genus EMILEIA Buckman, 1898

Type species. *Ammonites brocchii* (J. Sowerby, 1818, p. 233, pl. 202), by original designation of Buckman (1898, p. 456).

Emileia sp. indet.

Plate 1, fig. 1

Material. A single, fragmentary specimen (J9469), but relatively well preserved. Measurements cannot be made.



TEXT-FIG. 3. Suture lines of A, *Calliphylloceras heterophylloides* (Oppel), J9477, Bed 1; B, *Dorsetensia subsecta* Buckman, J9494, Bed 6; C, *Holcophylloceras zignodianum* (d'Orbigny), J9486, Bed 1; D, *Stephanoceras* (*Stephanoceras*) *scalare* Weisert, J9472, Bed 10; E, *Stephanoceras* (*Stephanoceras*) *triplex* Weisert, J9497, Bed 10. Scale bars 10 mm.

Description. A small fragmentary inner part, with a recrystallized and manganese-coated partly preserved shell. The specimen is cut by subsolution, which removed more than half the ammonite.

The umbilicus is very narrow, the whorl section is inflated with oblique, rounded umbilical wall and arched flank and venter. The dense ribbing consists of blunt, straight, rectiradial primary ribs reaching about one-third of the whorl height. The secondaries arise from the slightly elongated tubercles at the termination of the inner ribs. There are seventeen primary and fifty-nine secondary ribs on the 225° segment of the preserved outer whorl. The specimen is septate throughout, thus chambered part and the body chamber have been broken off. Only small parts of the suture line can be seen.

Remarks. The single, fragmentary specimen is insufficient for specific identification; however, some visible features suggest closer affinities. The very small umbilicus and the numerous, long primary

EXPLANATION OF PLATE 2

- Fig. 1. *Stephanoceras* (*Stephanoceras*) *leoniae* Schmidtil and Krumbeck. J9489; Közöskút; Bed 9, *Stephanoceras humphriesianum* Subzone; lateral view of a nearly complete specimen, $\times 1$.
 Fig. 2. *Holcophylloceras zignodianum* (d'Orbigny). J9468; Közöskút; Bed 1, *Teloceras blagdeni* Subzone; lateral view, $\times 0.7$.
 Fig. 3. *Stephanoceras* (*Stephanoceras*) *mutabile* (Quenstedt). J9486; Közöskút; Bed 5, *Stephanoceras humphriesianum* Subzone; lateral view, $\times 1$.
 Fig. 4. *Dorsetensia subsecta* Buckman, J9494; Közöskút; Bed 6, *Stephanoceras humphriesianum* Subzone; lateral view, $\times 0.6$.



GALÁ CZ, *Stephanoceras*, *Holcophylloceras*, *Dorsetensia*

ribs closely resemble the inner whorls of *Emileia greppini* Maubeuge, 1961. This species is usually represented by large specimens, but the type series (Greppin 1898, pls 1–3) also contain incomplete forms, showing the characteristic juvenile features.

Distribution. The type of *E. greppini*, according to Greppin (1898, p. 31) was collected from the 'Sauzei-Schichten' at Liestal, Switzerland. The *Sauzei* Zone age of these beds was supported recently by Ohmert *et al.* (1982, pp. 153–154). Parsons (1974, p. 159) cited *E. greppini* as a species characteristic in the *Sauzei* Zone.

In the Kőzöskút sequence the genus *Emileia*, even without closer identification, undoubtedly indicates the presence of the *Sauzei* Zone. This representation confines to a single bed (Bed 11), because the underlying Bed 12 yielded Toarcian ammonites, whereas Bed 10 above contained *Humphriesianum* Zone ammonites.

Family STEPHANOCERATIDAE Neumayr, 1875
Subfamily STEPHANOCERATINAE Neumayr, 1875
Genus and subgenus STEPHANOCERAS Waagen, 1869

Type species. *Ammonites Humphriesianus* (J. de C. Sowerby, 1825, p. 161, pl. 500, fig. 1), by subsequent designation of Buckman 1898, p. 454.

Stephanoceras (Stephanoceras) triplex Weisert, 1932

Plate 3, fig. 1; Text-fig. 3E

- 1932 *Stephanoceras triplex* Weisert, p. 52, pl. 16, fig. 1.
non 1961 *Stephanoceras* cf. *triplex* Weisert; Maubeuge, p. 108, fig. on p. 109.
v 1971 *Stephanoceras (Stephanoceras)* aff. *triplex* Weisert; Morton, p. 279, pl. 46, figs 1 and 2; pl. 47, figs 1 and 2.
1985 *Teloceras* (?) *triplex* Weisert; Schlegelmilch, p. 78, pl. 27, fig. 7.

Material. Two relatively well preserved, but fragmentary specimens.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr	S
J9497	225	225	60 (26.5)	94 (42)	114 (51)	—	—
		152	39 (25.5)	?60 (?39.5)	76 (50)	39	86
J9499	225	191	51 (27)	88 (46)	94 (52)	40	95
		152	40 (26.5)	64 (42)	76 (50)	36	92

Description. Large, robust form with moderately wide umbilicus. The figured specimen is a well preserved internal mould with fragmentary body chamber and manganese coating which has partly replaced the original shell. The width of the umbilicus remains constant (c. 50%) with growth. The whorl section is subcircular and hardly varies during growth. The umbilical slope and the lateral side are convex, and the venter is evenly rounded. The sculpture is a dense, regular ribbing. The primary ribs arise from the umbilical seam. The radial, slightly backwardly arched primaries are rounded on the internal mould, but probably sharp on the test. The primaries end in pointed, radially somewhat elongated, relatively small tubercles. These are situated at half of the height in the inner whorls, while the position of the tubercle row is gradually displaced lower, to about one-third the height of the body chamber. The number of primary ribs is fairly constant, i.e. 35–40 per whorl, but

EXPLANATION OF PLATE 3

- Fig. 1. *Stephanoceras (Stephanoceras) triplex* Weisert. J9497; Kőzöskút; Bed 10, *Stephanoceras humphriesianum* Subzone; lateral view, $\times 1$.
Fig. 2. *Nannolytoceras polyhelictum* (Böckh.) J9475; Kőzöskút; Bed 2, *Teloceras blagdeni* Subzone; lateral view, $\times 1$.



GALÁCZ, *Stephanoceras*, *Nannolytoceras*

somewhat increases on the outer whorls. Generally two secondary ribs arise from the tubercles, but eight to ten triplications may appear on each whorl, and additional intercalatories, starting at the row of the tubercles, also occur. The secondary ribs are rounded and projected slightly throughout the whorls and pass straight across the venter. The length of the body chamber cannot be measured, because apertural parts are missing in the studied material. The phragmocone ends at c. 150 mm diameter, and the longest preserved body chamber fragment comprises nearly one whorl.

The suture line is characteristic (Text-fig. 3E), showing narrow saddles and rather wide lobes. The lateral lobe is remarkably long and deeply incised. The umbilical elements are retracted.

Remarks. *S. triplex* belongs to the broadly-whorled *Stephanoceras brodiaei* group. The relatively wide umbilicus, the generally biplicate ribbing, the rather small tubercles, and the extremely long lateral lobe in the suture are all characteristic.

The species name '*triplex*' does not appear in the published work of Mascke (1907), in spite of the reference made by Weisert (1932, p. 52). Thus Weisert should be regarded as the author of this species, a procedure followed previously by others (e.g. Morton 1971, p. 279). The lectotype is the original of plate 16, figure 1 in Weisert (1932). This is a smaller specimen (see Schlegelmilch 1985, pl. 27, fig. 7), but nevertheless closely comparable with the inner whorls of the Kőzőskút forms. The number of the primaries is somewhat lower in the lectotype; on the other hand that form shows some irregularities in its sculpture. The form described by Maubeuge (1961, pp. 108–109 as *S. cf. triplex*) is not conspecific because of the wider whorls, somewhat narrower umbilicus and denser secondary ribbing. The forms figures by Morton (1971, pl. 46, figs 1 and 2; pl. 47, figs 1 and 2), though fragmentary and crushed, are near to the typical *S. triplex*.

Distribution. *Stephanoceras (S.) triplex* is a common and frequently recorded element in the *Humphriesianum* Zone faunas. Its subzonal distribution is to be ascertained. The Kőzőskút specimens came from Bed 10, i.e. from the *Humphriesianum* Subzone.

Stephanoceras (Stephanoceras) scalare Weisert, 1932

Plate 4, fig. 4; Text-fig. 3D

- v 1849 *Ammonites Humphriesianus*; Quenstedt, p. 180, pl. 14, fig. 10.
- 1858 *Ammonites Humphriesianus plicatissimus* Quenstedt, p. 298, pl. 54, fig. 3.
- p. 1887 *Ammonites Humphriesianus*; Quenstedt, p. 531, pl. 65, fig. 15 (only).
- 1932 *Stephanoceras scalare* Mascke; Weisert, p. 143, pl. 16, fig. 2; text-figs 7 and 8.
- 1937 *Stephanoceras scalare* Mascke; Horwitz, p. 261, pl. 11, fig. 3.
- ? 1938 *Stephanoceras scalare* Mascke em. Weisert; Schmidill and Krumbeck, p. 330, pl. 13, fig. 2; text-fig. 5.
- p. 1938 *Stephanoceras auerbachense* Schmidill and Krumbeck, p. 339, pl. 13, fig. 5 (only).
- 1946 *Cadomites Bigoti* Munier-Chalmas; Gardet and Gérard, p. 34, pl. 8, fig. 1.
- 1961 *Stephanoceras (Stephanoceras) scalare* Mascke em. Weisert; Krymholz, p. 112, text-fig. 14.
- non 1969 *Stephanoceras cf. scalare* Mascke; Maubeuge, p. 71, fig. on p. 71.
- 1973 *Stephanoceras cf. scalare* Mascke; Myczynski, p. 91, pl. 11, fig. 1; pl. 12, fig. 1.
- 1982 *Stephanoceras (Stephanoceras) scalare* Mascke em. Weisert; Azarian, p. 83, pl. 14, fig. 2; pl. 16, fig. 4; pl. 17, fig. 5.
- 1983 *Stephanoceras (Stephanoceras) scalare* Mascke emend. Weisert; Sandoval, p. 235, pl. 16, fig. 1.
- p. 1983 *Stephanoceras (Stephanoceras) scalare* Weisert (Mascke); Pavia, p. 89, pl. 12, fig. 5 (only).
- ? 1985 *Stephanoceras (Stephanoceras) scalare* Weisert; Rostovtsev, p. 141, pl. 39, fig. 1.
- non 1985 *Stephanoceras scalare* Weisert; Fernandez López, p. 283, pl. 29, fig. 1.
- 1985 *Stephanoceras (Stephanoceras) scalare* Loewe; Schlegelmilch, p. 70, pl. 22, fig. 4.

Material. Four specimens, two nearly entire internal moulds, one phragmocone and one body chamber fragment.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr	S
J9484	270	225	45 (20)	40 (18)	141 (65)	—	—
		141	34 (23)	?30 (?20·5)	81 (55)	47	—
J9498	250	235	45 (19)	?40 (?17)	153 (65)	—	—
		200	42 (21)	?40 (?20)	125 (62·5)	64	121
		136	33 (24)	?30 (?22)	71 (52)	47	—
J9483	131	131	32·5 (25)	32 (24·5)	72 (55)	48	—
		112	31 (27·5)	32 (28·5)	56·5 (50·5)	42	—
		89	30 (33·5)	30 (33·5)	43·5 (49)	37	—
		70	21 (30)	21 (30)	29·5 (42)	—	—
		52	18 (34·5)	19 (36·5)	20 (38·5)	—	—

Description. Large, planulate, serpentine form. The figured specimen is an almost complete, well preserved internal mould with partial manganese coating, which replaces the original shell. The umbilicus is very wide and gradually opens with individual growth: its width is *c.* 45–50 % in the inner, and 60–65 % in the outermost whorls. The shape of the whorl section also varies with growth, being somewhat depressed-circular in the inner whorls and compressed-oval on the body chamber. The umbilical slope is short and convex, the lateral sides are also convex, becoming slightly flattened on the outer whorls. The venter is convex and wider in the inner whorls. The ornament consists of dense ribbing. The inner ribs arise at the umbilical seam, run radially in the inner, and become slightly backwardly arched in the outer whorls. The number of primary ribs increases with growth: 30–35 in the inner whorls (at 50–70 mm diameter), and 60–65 in the outer whorls (at *c.* 190 mm diameter). The primary ribs end in slightly elongated, small, pointed tubercles around the lower third of the flanks. The long secondary ribs arise from the tubercles, are radial in the inner whorls and slightly prorsiradial on the body chamber. Here the number of the secondary ribs is smaller, two per primary. In the outermost whorl simple ribs and intercalatories appear, arising freely at the level of the tubercles. The rounded secondaries run straight across the venter. The body chamber is very long, beginning at 130–140 mm diameter and consisting of more than one and a half whorls. The apertural part is missing in all specimens.

Entire suture line cannot be seen in either specimen. The clearly visible sutural portions show moderately deep, relatively broad lateral, and moderately retracted umbilical lobes (Text-fig. 3*D*.).

Remarks. The synonymy of early citations of this form was discussed in detail by Pavia (1983, pp. 89–91). However, the origin of the species' name is mysterious. In Weisert (1932, p. 143) the whole name is '*Stephanoceras scalare* Mascke sp. 1903, *em.* Weisert 1931'. Even the 1903 date is strange, because although this is the year when Mascke defended his thesis, the work itself was published in 1907, so this is the valid citation date. On the other hand, the species' name '*scalare*' does not appear in the publication. This is probably why subsequent authors used the *S. scalare* Mascke or the *S. scalare* Weisert versions.

The photograph of the holotype was first published by Weisert (1932, pl. 16, fig. 2). Nevertheless, Weisert (1932, p. 143) had at least one additional specimen, from which measurements were recorded. These show that this specimen is probably not conspecific. More recently Pavia (1983, pl. 12, fig. 5) published a photograph of the plaster cast of the holotype and also recorded its dimensions. However, the three other forms figured by Pavia (1983, pl. 12, figs 1, 3, 4) differ significantly from the type in size and sculpture and thus are regarded here as non-conspecific.

Fragments of *S. scalare* were figured by Horwitz (1937) and by Myczynski (1973) from the Pieniny Klippen Belt, Polish Carpathians, and by Gardet and Gérard (1946, pl. 8, fig. 1, as '*Cadomites Bigoti*') from the Middle Atlas Range. One of the best descriptions of the species is by Krymholz (1961, p. 112), who recorded it from the Northern Caucasus. Good specimens were described by Azarian (1982) and a fragment of a very similar form was figured by Rostovtsev (1985). Sandoval (1983, p. 235, pl. 16, fig. 1) recorded the species from the Betic Cordilleras. The identity of the two specimens figured by Schmidtil and Krumbeck (1938, pl. 13, fig. 2; text-fig. 5; pl. 13, fig. 5 – the latter as *Stephanoceras auerbachense*) is doubtful because of their poor preservation. The ammonite figured by Maubeuge (1969, pl. 71, No. 66959, as *S. cf. scalare*) is a badly preserved fragmentary specimen with coarse ribbing and short, bulky primaries.

Westermann and Riccardi (1979, p. 155) regarded, with question marks, *S. scalare* (and other *Stephanoceras* species) as synonyms of *S. pyritosum* (Quenstedt). They published a photograph of the type of this latter species: from this it is clear that the number of the primary ribs remains low throughout the whorls, whereas it is higher in all stages in typical *Stephanoceras scalare*.

The features mentioned in the description (i.e. wide umbilicus, dense ribbing, whorl section becoming compressed on the outermost whorl, etc.) clearly distinguish this form from other species of the *Stephanoceras humphriesianum* group. *S. humphriesianum* itself is a rare ammonite, which can be characterized by shorter inner ribs with clearly distinguished, rounded tubercles and regularly three, or rarely four, secondaries. Another, similar form of this group is *S. rhytus* (Buckman 1921, pl. 250). However, this species is characterized by strongly rectiradiate primaries and strongly projected bundles of secondaries, and these result in a distinguishing, marked break in the sculpture.

Distribution. *S. scalare* is apparently a widely distributed *Stephanoceras*. The type probably came from the *Humphriesianum* Zone of Bopfingen, South Germany (see Pavia 1983), the other described forms are similarly recorded from the *Humphriesianum* Zone. Parsons (1976, pp. 131, 134) mentioned *S. cf. scalare* from the English *Humphriesianum* and *Romani* Subzones. Sandoval (1983, p. 236) found the species in the upper part of the *humphriesianum* Zone. Thus the species occurs in wide geographic distribution from North Africa to the Caucasus, both in Mediterranean and northwest European faunas, in the *Humphriesianum* Zone.

The Kőzöskút species came from Beds 10 and 4 of the *Humphriesianum* Subzone.

Stephanoceras (*Stephanoceras*) sp.

Plate 1, fig. 3.

Material. A single, well-preserved, entire, but somewhat corroded specimen.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr
J9488	169	159	35 (22)	38 (24)	99 (62)	—
		130	30 (23)	34 (26)	73.5 (56.5)	—
		107	27 (25)	37 (34.5)	57.5 (54)	41

Description. A relatively large serpenticone internal mould. The umbilicus is shallow and extremely wide, especially on the outer whorls. The whorl section is subcircular, high-oval on the body chamber. The umbilical wall is convex, the flanks are slightly rounded, and the venter is highly arched. Maximum width can be measured around the lower third of the whorl height. The ornament is formed by dense ribbing. The primary ribs are rounded and short, at about one-quarter their height they branch into three or rarely two secondaries. The secondary ribs are straight, rounded and slightly rectiradiate on the body chamber. At 107 mm diameter the number of primary ribs is forty-one, and here the primary:secondary rib ratio is 18:48 for a half whorl. On the visible inner whorls the primary ribs are longer, prorsiradiate, and terminate in tubercles. The body chamber occupies the entire last whorl, with a slightly expanding, smooth collar.

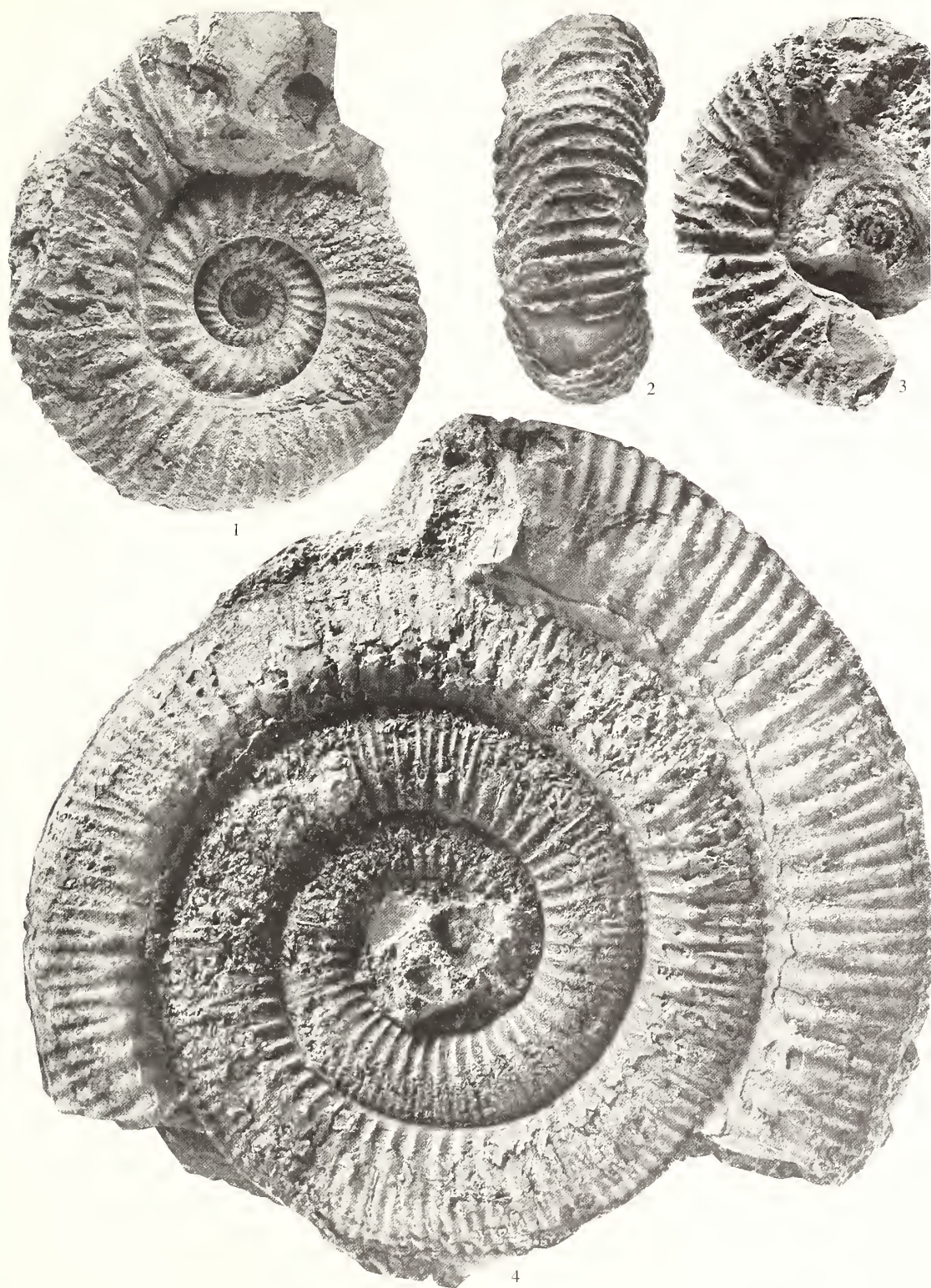
The entire suture line cannot be seen, but the visible parts show typical *Stephanoceras*-like divided saddles, deep lateral lobe and strongly retracted umbilical lobe.

EXPLANATION OF PLATE 4

Fig. 1. *Stephanoceras* (*Normannites*) sp. aff. *fortis* Pavia. J9480; Kőzöskút; Bed 3, *Teloceras blagdeni* Subzone; lateral view of a complete adult microconch, $\times 1$.

Figs 2 and 3. *Stephanoceras* (*Normannites*) *orbigny* Buckman. J9463; Kőzöskút; Bed 3, *Teloceras blagdeni* Subzone; 2, lateral and 3, ventral views of an adult microconch, $\times 1$.

Fig. 4. *Stephanoceras* (*Stephanoceras*) *scalare* Weisert. J9498; Kőzöskút; Bed 10, *Stephanoceras humphriesianum* Subzone; lateral view of an almost complete specimen, $\times 0.7$.



GALÁ CZ, *Stephanoceras*

Remarks. Because of incomplete preservation, this single specimen is insufficient for specific determination. A similar form is that described by Pavia (1983, p. 97, pl. 14, fig. 6) from the *Humphriesianum* Zone of Bayeaux. He assigned this specimen to *Stephanoceras tenuicostatum*; however, this latter species is smaller, has distant and longer primary ribs with tubercles throughout the internal mould of the body chamber. The individual features of the Normandy species are close to those of the Kőzőskút form; nevertheless, designation of a new species would need further material.

Distribution. The Kőzőskút specimen came from Bed 9, i.e. from the *Humphriesianum* Subzone. The Normandy specimen was collected from the condensed *Humphriesianum* Zone of Bayeux.

Stephanoceras (Stephanoceras) leoniae Schmidtil and Krumbeck, 1938

Plate 2, fig. 1

- 1938 *Stephanoceras leoniae* Schmidtil and Krumbeck, p. 343, pl. 11, fig. 4.
non 1949 *Stephanoceras leoniae* Schmidtil and Krumbeck; Maubeuge, p. 173, pl. 13.

Material. Two incomplete, relatively well preserved specimens.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr
J9473	117	117	32.5 (27.5)	32 (27.5)	58 (49.5)	—
		88.5	28.5 (32)	31 (35)	38 (43)	—
J9489	113	113	34 (30)	35 (31)	53 (47)	—
		92	31 (33.5)	36 (39)	42 (45.5)	31

Description. A relatively small stephanoceratid. The figured specimen is a corroded internal cast with partial manganese coating. The umbilicus is moderately wide, the whorl section is circular with convex umbilical side and flanks, and with evenly arched venter. The sculpture is only partially visible. The straight, slightly prorsiradiate primary ribs arise at the umbilical seam and their number somewhat increases on the outer whorl. The primaries are slightly strengthened at the lower third of the flanks, without forming true tubercles. At this level the slightly curved, generally radial, rounded secondary ribs appear. Their strength is variable; those arising from the thickened primaries are stronger, whereas those starting freely are somewhat weaker. These differences disappear towards the venter. The better preserved half of the penultimate whorl bears fifteen primary and about forty-eight secondary ribs. The slightly contracted body chamber occupies two-fifths of the preserved last whorl; the aperture is missing. The suture line cannot be seen.

Remarks. The type (Schmidtil and Krumbeck 1938, pl. 11, fig. 4) is an incomplete, poorly preserved specimen of 90 mm diameter. The original description mentioned the dense ribbing and strong secondaries as characteristic. The type specimen is wholly septate, but the excentric umbilical seam indicates that the missing part was probably the body chamber. Thus this is a relatively small form, comparable to the Kőzőskút specimens. The ribbing is also similar, showing the smoothed tubercles mentioned in the original description.

The ammonite assigned to this species by Maubeuge (1949, pl. 13) differs in being more evolute, compressed (its Wb:Wh ratio is 0.85, as against 1.1 of the type) and having lowly situated, slightly elongated tubercles instead of real primary ribs.

Sandoval (1983, pp. 241–243) and also Schlegelmilch (1985, p. 72) regarded *S. leoniae* as a synonym of *Stephanoceras zogenreuthense*, another species of Schmidtil and Krumbeck. However, the type of this latter is different, having denser ribbing, stronger primaries and distant tubercles.

Distribution. The horizon of the type is uncertain within the 'Humphriesianum-Schichten' of South Germany. The Kőzőskút specimens came from Bed 9, i.e. from the *Humphriesianum* Subzone.

Stephanoceras (Stephanoceras) mutabile (Quenstedt, 1886)

Plate 1, fig. 2; Plate 2, fig. 3

- 1886 *Ammonites Humphriesianus mutabilis* Quenstedt, p. 537, pl. 66, fig. 5.
 non 1909 *Stephanoceras mutabile* Quenstedt; Lissajous, p. 181, pl. 6, fig. 14.
 1932 *Stephanoceras mutabile* Quenstedt; Weisert, p. 153, pl. 17, fig. 6; text-figs 15 and 16.
 v 1971 *Stephanoceras (Stephanoceras) mutabile* Quenstedt; Morton, p. 273, pl. 40, figs 5–10; text-fig. 2A.
 ? 1983 *Stephanoceras (Stephanoceras) mutabile* (Quenstedt); Sandoval, p. 238, pl. 17, fig. 3; text-fig. 99B.
 p. 1983 *Stephanoceras (Stephanoceras) gr. umbilicum* (Quenstedt); Pavia, p. 100, pl. 12, fig. 2 (only).
 1985 *Stephanoceras umbilicum* (Quenstedt); Fernandez López, p. 278, pl. 27, fig. 3; text-fig. 29H.
 1985 *Stephanoceras (Stephanoceras) mutabile* (Quenstedt); Schlegelmilch, p. 72, pl. 25, fig. 1.

Material. Two incomplete and fragmentary internal moulds.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr/2	S/2
J9496	115	115	40 (35)	50 (43.5)	49 (43)	18	47
		48	30 (35)	37 (43.5)	35 (41)	—	—
J9486	94	94	32 (34)	?44 (?47)	33.5 (35.5)	18	51

Description. Medium-sized forms. The two figured specimens are fragmentary, the bigger is a corroded internal mould, the smaller is a similarly badly preserved specimen, with partial manganese coating. The umbilicus is relatively narrow and deep, its width is constant during growth. The whorl section is subcircular, with steep, slightly convex umbilical walls and widely arched venter. The sculpture consists of dense ribbing. The primary ribs arise from the umbilical seam, are rounded on the internal mould, but sharp on the shell. The number of the slightly rectiradial, backwardly arched primaries is eighteen and sixteen on the preserved last and penultimate half-whorl of the bigger specimen. The primary ribs end in sharp, circular tubercles at the lower third of the flank. The tubercles are weaker on the internal mould. Two to three secondary ribs start from the tubercles, i.e. there are forty-seven secondaries on the last half whorl. The secondary ribs are radial, only slightly curving. The smaller specimen is wholly septate, the larger one shows a very short part of the body chamber, which begins at c. 106 mm diameter. The suture line cannot be seen clearly.

Remarks. Quenstedt (1886–87, pl. 66, fig. 5) figured only the ventral view of the holotype; later Weisert (1932, pl 17, fig. 6) published a photograph of the lateral side. More recently Schlegelmilch published both views of the holotype (1985, pl. 25, fig. 1). These show clearly that its characteristics are the relatively narrow umbilicus and the dense ribbing with low tubercle row (see also Morton 1971, p. 274). Pavia (1983, pp. 100–101) regarded *S. kreter* (Buckman), *S. mutabile* (Quenstedt) and *S. umbilicum* (Quenstedt) as a single group, suggesting a transient position for *S. mutabile*, on the basis of the umbilical width and the length of the primary ribs.

An additional feature of the species is its relatively small size. As Westermann and Riccardi pointed out (1979, p. 158), a part of the last whorl of the holotype is body chamber. The Közöskút specimens, though fragmentary, correspond well with the figures of the holotype. These are also small forms: one of the specimens shows the end of septation at 106 mm diameter.

S. mutabile is a commonly recorded but rarely illustrated species. The ammonite figured by Lissajous (1907–1912, pl. 6, fig. 14) from the *Parkinsoni* Zone is clearly different, probably being the inner whorls of a *Cadomites* sp. Good figures were published by Schmidtil and Krumbeck (1938). Sandoval (1983, pl. 17, fig. 3) figured a specimen of strongly corroded outer whorls, thus difficult to identify. However, the recorded dimensions and the cross-section show a closely allied form.

Distribution. The holotype came from the middle part of the *Humphriesianum* Zone (see Morton 1971, p. 275, and Pavia 1983, p. 102). Other records indicate the same stratigraphic level. Parsons (1976, p. 139) cited the species as a characteristic form in the *Humphriesianum* Subzone. The Közöskút specimens came from Beds 9 and 5 of the *Humphriesianum* Subzone.

Stephanoceras (Stephanoceras) sturani Pavia, 1983

Plate 1, fig. 5

1983 *Stephanoceras (Stephanoceras) sturani* Pavia, p. 94, pl. 13, figs 4 and 6.

Material. Two incomplete, fragmentary specimens (J9461–J9462) of poor preservation. Precise measurements cannot be made.

Description. The figured specimen (J9461) is a fragmentary internal mould with subsolved inner whorls and an incomplete, slightly distorted body chamber. The umbilicus is narrow and deep in the inner whorls, becoming excentric and wide on the last whorl. The whorl section is subcircular with low, oblique umbilical wall rounding into the convex whorl-side without shoulder. The venter is widely arched. The ribbing is extremely dense, consisting of short, lamellar primaries, which end in radially elongated tubercles below the lower third of the flanks. From the tubercles arise the secondaries, which are sharp on the flanks and rounded on the venter. Both the primary and the secondary ribs are radial. On the preserved quarter of the last whorl there are seventeen primary and forty-one secondary ribs.

The suture line cannot be seen clearly, only the strongly retracted umbilical elements are visible.

Remarks. The specimens closely resemble the recently designated species of Pavia. With its narrowly coiled inner and middle whorls, excentric body chamber and very dense sculpture this is a species from an incompletely known group of Mediterranean stephanoceratids. Another member of this group is described above as *Stephanoceras (S.)* sp.

Description. The holotype of this species came from the *Blagdeni* Subzone of Digne, SE France, and Pavia (1983, pl. 13, fig. 4) described an additional specimen from the *Humphriesianum* Zone of Normandy. The Kőzőskút specimens came from Bed 3, i.e. the *Blagdeni* Subzone.

Subgenus NORMANNITES Munier-Chalmas, 1892

Type species. *Normannites orbignyi* Buckman, 1908 = *Ammonites Braikenridgii* d'Orbigny (non Sowerby), 1845, p. 400, pl. 135, figs 3 and 4.

Stephanoceras (Normannites) orbignyi Buckman, 1908

Plate 4, figs 2 and 3

- v 1845 *Ammonites Braikenridgii* Sowerby; d'Orbigny, p. 400, pl. 135, figs 3 and 4 (only).
- 1908 *Normannites Orbignyi* Buckman, p. 146.
- 1927 *Normannites orbignyi* Buckman; Buckman, pl. 734, figs 1–3.
- ?1937 *Cadomites Orbignyi* Buckman; Gillet, p. 86, text-fig. 62.
- ?1937 *Normannites Orbignyi* Buckman; Horwitz, p. 265, pl. 12, fig. 2.
- non 1939 *Normannites Orbignyi* Buckman; Roché, p. 219, pl. 1, fig. 5a–b.
- 1954 *Normannites (Normannites) orbignyi* Buckman, and subsp.; Westermann, pp. 135–152, pl. 5, figs 3 and 4; pl. 6, figs 1, 3–5; pl. 7, figs 1–5; pl. 8, fig. 1; text-figs 35–44.
- non 1971 *Stephanoceras (Normannites)? orbignyi* Buckman; Morton, p. 282, pl. 51, figs 1 and 2.
- non 1973 *Normannites (Normannites) orbignyi* Buckman; Imlay, p. 82, pl. 41, figs 9, 10, 18, 20.
- v 1978 *Normannites orbignyi* Buckman; Dietl et al., p. 10, text-fig. 3a.
- 1983 *Normannites (s.s.) orbignyi* Buckman; Pavia, p. 142, pl. 27, figs 3 and 5.
- 1985 *Normannites orbignyi* Buckman; Fernandez López, p. 321, pl. 34, fig. 1; text-fig. 36E.
- 1985 *Stephanoceras (Normannites) orbignyi* Buckman; Schlegelmilch, p. 73, pl. 25, fig. 3.

Material. A single, fragmentary internal mould of a damaged individual (J9463). Measurements would be difficult to make and misleading.

Description. The size of the specimen is c. 65 mm, and only the last half whorl is well preserved. The specimen is a small microconch with moderately wide umbilicus and somewhat depressed-oval whorl section. The well preserved part, which is the last half segment of the body chamber is slightly contracted with decreasing width

and height. The umbilical wall is steep, arched, the flanks are convex and the venter is widely arched. The sharp, prorsiradiate, slightly curved primary ribs arise at the umbilical seam. There are fifteen primaries on the last half whorl. The primary ribs end in radially elongated, pointed tubercles near the middle of the whorl height, giving rise to usually two secondary ribs. Some intercalatories also appear so the primary:secondary rib ratio is 13:34 on the last half whorl. An important feature is that the level of the tubercles gradually sinks on the body chamber. The secondaries are straight and cross the venter perpendicularly. Despite the bad preservation, some parts of the ornament are visible on the inner whorls. At c. 20 mm diameter the estimated number of primary ribs is twenty. The aperture cannot be seen properly, because the lappets are not preserved on the internal mould. However, the lateral inflation probably represents the base of the lappet. The suture line cannot be studied.

Remarks. Buckman (1908, p. 146) distinguished this species on the basis of the '*Ammonites Braikenridgii*' figure of d'Orbigny. He published the photograph of the type in 1927 (in 1909–30, pl. 734). Subsequently Westermann (1954, p. 136) named this specimen [unnecessarily] as the 'neotype'.

Westermann (1954), on the basis of whorl section and rib density, split *N. orbignyi* into four subspecies. However, these features are so variable in stephanoceratids in general, and *Normannites* in particular, that *N. orbignyi* is better regarded as a species of wide morphological variability (see also Westermann 1964). In this respect the Közöskút specimen is a form with a slightly wider umbilicus, but otherwise matching the type rather closely.

Of the rather common citations of *N. orbignyi*, the specimen of Horwitz (1937, pl. 12, fig. 2) is a very poorly preserved ammonite, insufficient for specific identification. The description and drawing of Gillet (1937, p. 86) is similarly insufficient to decide on specific identity. The specimen figured by Roché (1939, pl. 1, fig. 5) is a big form with an extremely wide umbilicus, and thus certainly not conspecific. The poorly preserved specimen of Morton (1971, pl. 51, figs 1 and 2), with large, elevated tubercles and dense secondary ribbing is also different.

Distribution. The type came from the *Epalxites* hemera of the *Humphriesianum* Zone of Dorset, which corresponds to the *Humphriesianum* Subzone (see Parsons 1976, p. 116). Other references mention the species from the *Blagdeni* Subzone and from the basal *Niortense* Zone. The Közöskút specimen came from Bcd 3, i.e. from the *Blagdeni* Subzone.

Stephanoceras (Normannites) sp. aff. fortis Pavia, 1983

Plate 4, fig. 1

aff. 1983 *Normannites fortis* Pavia, p. 146, pl. 28, figs 2, 3, 6.

Material. A single, well preserved internal mould.

Measurements.

	MDm	Dm	Wh	Wb	Ud	Pr	S
J9480	77	77	27 (35)	31 (40)	35 (45)	35	68
		63.5	20 (31.5)	26 (41)	28 (44)	28	—

Description. A relatively large form. The umbilicus is moderately wide, opening slightly on the last half whorl. The whorl section is depressed, rounded, becoming more depressed near the end of the body chamber by contraction. The umbilical wall and the flanks are evenly convex, the ventral side widely arched. The sculpture consists of regular ribbing. The straight, prorsiradiate primary ribs are rounded on the internal cast, begin on the umbilical wall and reach the half of the flanks on the phragmocone, and the third on the body chamber, respectively. At the endings they are strengthened without tubercles, and branch into secondaries. There are thirty-five primaries on the outermost whorl, twenty-eight on the penultimate whorl and the same number on the preceding ones. The secondary:primary rib ratio is 68:35 on the last whorl, i.e. some singular ribs run onto the venter. The secondary ribs are straight and prorsiradiate, crossing the venter perpendicularly. The length of the body chamber is four-fifth of a whorl, the peristome is partially preserved, showing a slightly flared ventral ridge and short lateral lappets. Details of the suture line cannot be seen.

Remarks. Despite good preservation, identification with known *Normannites* species was apparently not possible. Special features are the low number of primary ribs in the middle whorls, the relatively numerous singular ribs on the outer whorl, and the complete lack of tubercles. This latter is characteristic to the '*Parallites*' of Westermann (1954). However, *Parallites* species show denser ribbing and narrower umbilicus. Of the *s.s.* *Normannites*, *N. vulgaricostatus pfaffi* Westermann (1954, p. 176, pl. 10, fig. 5) is similar, but this is smaller and has a narrower umbilicus and arched primary ribs. Closest similarity appears to be with *N. fortis*, a species of Pavia (1983, p. 146) from Digne. The most closely allied form is the paratype on plate 28, fig. 3 of Pavia. This differs from the holotype (*loc. cit.*, pl. 28, fig. 6) in having denser ribbing and undeveloped tubercles: features just present in the form described here. A very similar specimen was figured by Fernandez López (*Normannites cf. fortis*, 1985, pl. 33, fig. 3) from the *Banski* Subzone of the *Niortense* Zone from the Iberian Cordilleras.

Distribution. All specimens of *Normannites fortis* Pavia came from the uppermost *Humphriesianum* Zone; the Kőzőskút specimen was yielded by Bed 3, the *Blagdeni* Subzone.

Genus STEMMATOCERAS Mascke, 1907

Type species. *Ammonites Humphriesianum coronatus* Quenstedt, 1886, p. 539, pl. 66, fig. 1 = *Stephanoceras Frechi* Renz, 1904, p. 77, by original designation of Mascke, 1907, p. 30.

Stemmatoceras frechi (Renz, 1904)

Plate 5, figs 1–3

- 1886 *Ammonites Humphriesianus coronatus* Quenstedt, p. 539, pl. 66, fig. 11.
 1904 *Stephanoceras Frechi* Renz, p. 77.
 p. 1932 *Stemmatoceras coronatum* Quenstedt; Weisert, p. 159, pl. 18, fig. 4 (only).
 1938 *Stemmatoceras coronatum* Quenstedt; Schmidill and Krumbeck, p. 345, pl. 12, fig. 2.
 1939 *Cadomites Quenstedti* nomen novum Roché, p. 205.
 non 1951 *Stephanoceras quenstedti* Roché; Maubeuge, p. 64, pl. 14, fig. 2.
 ?1951 *Stephanoceras aff. quenstedti* Roché; Maubeuge, p. 64, pl. 5, fig. 4.
 ?1967 *Stemmatoceras (Stemmatoceras) aff. frechi* (Renz); Seyed-Emami, p. 136, pl. 4, fig. 22; pl. 15, fig. 3a–c.
 non 1969 *Stemmatoceras aff. frechi* Renz; Pavia, p. 447, fig. 3/4.
 non 1983 *Stemmatoceras (Stemmatoceras) sp. cf. S. (Stm.) frechi* Renz; Sandoval, p. 252, pl. 12, fig. 1; text-fig. 99i.
 non 1985 *Stemmatoceras coronatum* (Quenstedt); Rostovtsev, p. 143, pl. 40, fig. 1; pl. 41, fig. 1.
 1985 *Teloceras frechi* (Renz); Schlegelmilch, p. 77, pl. 27, fig. 6.

Material. Several well preserved specimens of which four were sufficient for detailed study.

Measurements

	MDm	Dm	Wh	Wb	Ud	Pr	S
J9482	145	131	29 (23)	?58 (?45)	68 (52)	35	87
		112	29 (26)	56 (50)	55 (49)	29	84
		83	24 (29)	46 (55.5)	38 (46)	26	—

EXPLANATION OF PLATE 5

Figs 1–3. *Stemmatoceras frechi* (Renz). 1 and 2, J9459; Kőzőskút; Bed 9, *Stephanoceras humphriesianum* Subzone; dorsal and lateral views of a smaller specimen. 3, J9482; Kőzőskút; Bed 4, *Stephanoceras humphriesianum* Subzone; lateral view of an adult form. All $\times 1$.



GALÁČZ, *Stenmatoceras*

	MDm	Dm	Wh	Wb	Ud	Pr	S
J9479	133	133	32 (24)	68 (51)	71 (53.5)	—	—
		112	28 (25)	63 (56)	54.5 (48.5)	—	—
J9466	117	117	32 (24)	68 (51)	59 (50)	33	74
		100	32 (32)	58 (58)	52.5 (52.5)	31	—
J9495	90	90	25 (28)	54 (60)	42 (47)	29	72
		75	21.5 (29)	42 (56)	34.5 (41)	28	—

Description. Medium to large forms of evolute coiling, with deep, relatively wide umbilicus, which becomes even wider with growth. The whorl section is depressed oval, the height:width ratio is *c.* 0.5 throughout the whorls. The umbilical slope is steep, the flanks are low, and the venter is broadly arched. The sculpture consists of relatively dense primary and secondary ribs. The primaries are long, radial, but slightly projected in the inner whorls. In the middle whorls the primary ribs are somewhat sharper on the internal mould. The number of primaries is nearly constant, being twenty-eight at 75 mm and thirty-five at 131 mm diameters, respectively. The primary ribs end in sharp tubercles. The row of tubercles is situated above the middle of the flanks in the internal and middle whorls, then lowers to middle position on the body chamber. Radial or slightly projected secondary ribs arise from the tubercles. The secondary:primary rib ratio is 2.8 to 2.4 on the phragmocone and 2.2 on the body chamber. The specimens studied are incomplete, with the outer whorls partially preserved, so the entire length of the body chamber and the aperture cannot be studied. One large specimen shows septation at 133 mm largest preserved diameter, other specimens show the beginning of the body chamber at 95 and 115 mm.

Suture line cannot be clearly seen on either specimen, only some characteristic stephanoceratid portions are visible.

Remarks. The date of designation of *Stemmatoceras frechi* by Renz is usually regarded as 1913 (see e.g. Westermann and Riccardi 1979, p. 166); however, the first explicit reference to this form by this name was made by Renz in 1904, p. 77. The status of Quenstedt's form as the type of the genus *Stemmatoceras* has been commonly neglected and thus most references are misinterpretations (see synonymy). Weisert (1932), while refiguring the original specimen of Quenstedt, also illustrated another form (pl. 18, fig. 1, text-fig 23) from Beuren, now in the collections of the Stuttgart Museum (No. 22206), and this is a normal *Stephanoceras s.s.* Roché (1939, p. 205) recognized the difficulty arising from the use of name '*coronatum*' and so he introduced a new name, '*Cadomites Quenstedti*', for the form of Quenstedt, which is thus an objective synonym. This name was applied by Maubeuge (1951) for a serpenticone *Stephanoceras s.s.* (pl. 14, fig. 2), and for a badly preserved, specifically undeterminable ammonite (pl. 5, fig. 4). The form figured by Rostovtsev from the Transcaucasus (1985, pl. 40, fig. 1; pl. 41, fig. 1) is a robust stephanoceratid, close to *Teloceras acuticostatum*.

Distribution. The type came from the *Humphriesianum* Zone of Eningen, Swabia, and Kumm (1952) suggested the species (by the name *Stephanoceras coronatum* (Quenstedt) as a guide in the lowermost part of the *Humphriesianum* Zone (see Westermann 1967, p. 142). However, Sturani (1971, p. 50) stated, that *Stemmatoceras frechi* has a long vertical range throughout the *Humphriesianum* Zone, thus this species never became widely used as subzonal index.

The Közőskút specimens came from Beds 9, 4, 3 and 2, i.e. from both the *Humphriesianum* and *Blagdeni* Subzones, thus confirming the extended range of the species.

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THE ORDOVICIAN GRAPTOLITES *AZYGOGRAPTUS* AND *JISHOUGRAPTUS* IN SCANDINAVIA AND BRITAIN

by A. J. BECKLY and JÖRG MALETZ

ABSTRACT. Two groups within *Azylograptus* are identified on the presence or absence of adpressed growth of the 1st along the sicula. The second group has an unusual facies association and this is interpreted to reflect adaptation to a shoreward, and possibly *r*-selective environment. Adaptation to such an environment is argued to have the potential to affect proximal development and consequently the evolutionary origins of this group are obscure. The subgenera previously erected are not used because of difficulties with the type species. Features of the proximal development are the main characters used to distinguish the species, and all the previously named Scandinavian and British species are redescribed except for *A. coelebs* for which no reliable specimens can be found. Three new species are described, *Azylograptus minutus*, *Jishougraptus novus* and *J. lindholmae*. *Jishougraptus* is recognized for the first time outside China, and the first specimens of *Azylograptus* from South America are illustrated.

THE genus *Azylograptus* was established by Nicholson (1875) with *A. lapworthi*, from the Skiddaw Slates of the English Lake District, as the type species. The single-stiped morphology and simple thecal form make the genus easily recognizable, but the differences between species are relatively subtle and identification has been further complicated by the lack of modern descriptions for many of the species from Scandinavia and Britain. This paper redescribes the type material for the species from these areas, and three new species are described from Scandinavia, two of which are placed in *Jishougraptus*. A summary of the other species that have been placed in *Azylograptus*, but which are not described in this paper, is given, with a brief comment on their probable validity as species and placement in *Azylograptus*.

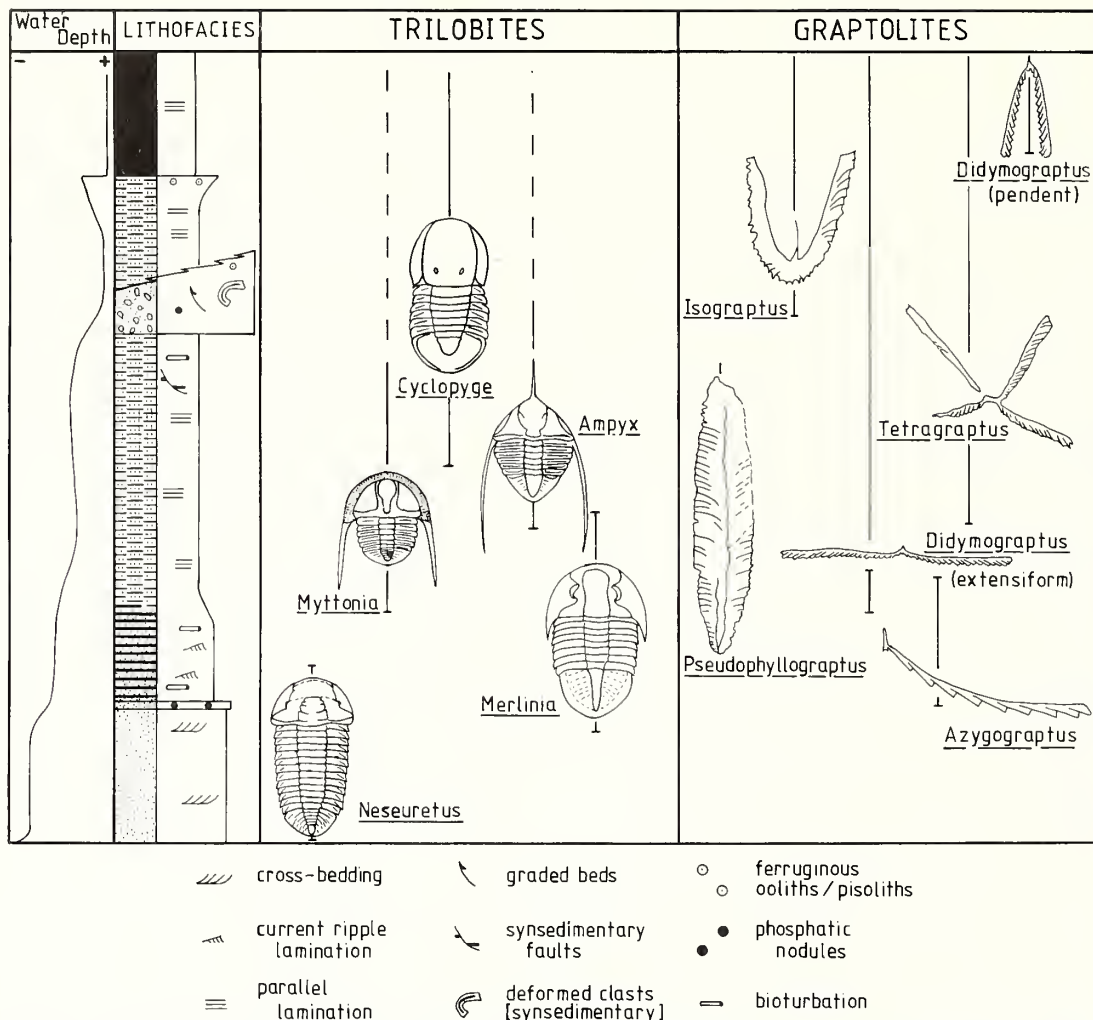
Azylograptus has been recognized as one of the most characteristic genera of the Atlantic Province during the Arenig (Skevington 1973), and Fortey (1984) suggested that the genus belonged to the epiplanktonic fauna which allowed it to penetrate more shoreward than other graptolite genera (Fortey and Owens 1987, p. 278; Chen and Yang 1987, fig. 2a). We examine the distribution of the genus not only with regard to palaeogeography, but also with respect to facies association. This provides a guide to the ecology of the genus from which its evolution and biostratigraphic usefulness are reviewed.

DISTRIBUTION

Facies association

Biofacies association. In Wales *Azylograptus* is generally the first graptolite to occur in the transgressive succession above the basal Arenig unconformity, where it commonly forms abundant, monospecific assemblages (Fortey and Owens 1987; Beckly 1987). Locally *Azylograptus* is replaced in this position by extensiform graptolites comparable to *D. simulans* (Beckly 1985; Zalasiewicz 1986) which share a number of characteristics with *Azylograptus*: low thecal inclination, metasicular origin of the 1st (Beckly 1985) and the production of synrhabdosomes (Zalasiewicz 1984).

The relationship of the Welsh occurrences to the trilobite communities identified by Fortey and Owens (1978) also indicates a position low in a transgressive succession (Text-fig. 1). *Azylograptus* typically occurs shortly above sandstone beds that either yield a fauna indicative of the *Neseuretus*



TEXT-FIG. 1. Graptolite and trilobite distribution within the Arenig transgressive succession of North Wales.

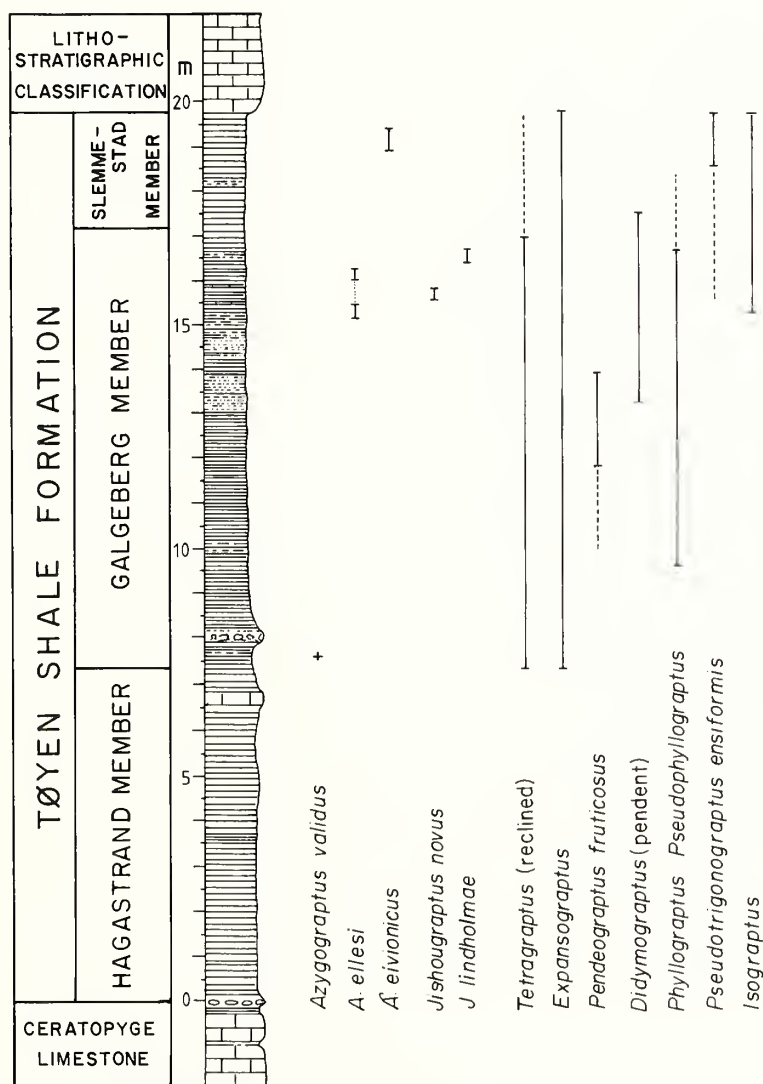
Community (e.g. Bangor Area) or for which it is implied by the presence of *Cruziana* (cf. Fortey and Morris 1982): in the Arenig area rare specimens of *Azygograptus* are associated with a *Neseuretus* fauna. The raphiophorid community generally overlies the occurrences of *Azygograptus* in North Wales and the associates of *A. eivonicus* in the Aberdaron Area (see *A. eivonicus*, p. 904) suggest a position at the shoreward limit of this community.

These occurrences contrast with those of *Azygograptus* in Scandinavia where the genus is generally associated with diverse graptolite faunas, which occasionally indicate the deep water isograptid biofacies (cf. Fortey and Cocks 1986). However, *A. eivonicus* is the only species common to both areas and in the Toyen Shale this species occurs just below the *Orthoceras* Limestone, which has been taken as indicative of a regressive eustatic event (Fortey 1984). *A. suecicus* appears to have a more restricted distribution and to have a positive association with *I. gibberulus sensu* Moberg, which may reflect some degree of biofacies association.

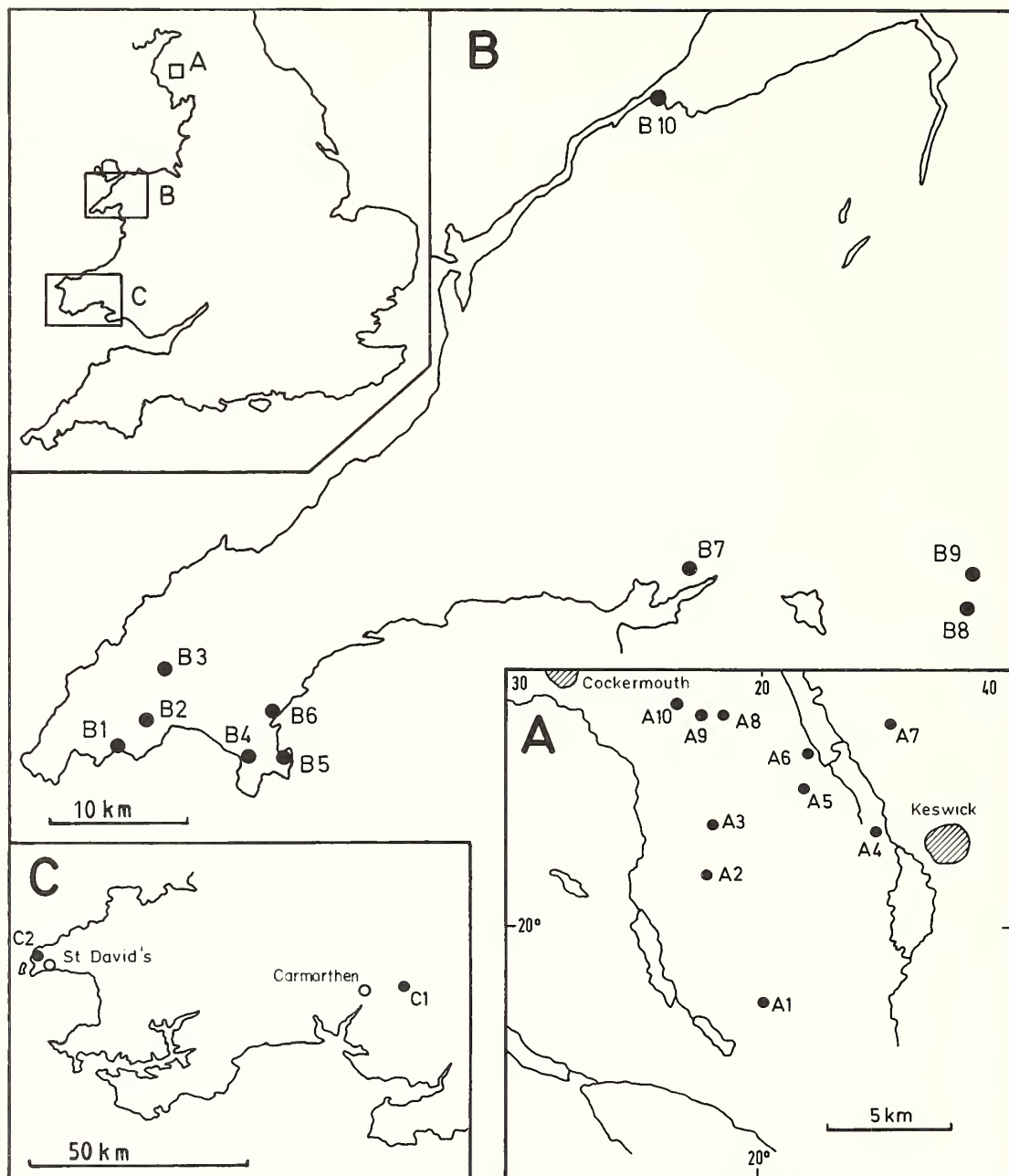
In the English Lake District *Azygograptus* occurs in both low diversity to monospecific assemblages and as a member of more diverse faunas. However, even among the more diverse

faunas *Azygograptus* tends to occur as fairly abundant populations on certain bedding-planes from which other species are absent or rare. In addition, adjacent graptolite assemblages are often slightly unusual and difficult to correlate (e.g. Barf and Hodgson How Quarry), and may reflect a slightly different biofacies. Interestingly, *D. simulans*, which appears to favour a similar facies to *Azygograptus* in North Wales, also occurs at Barf. The only suggestion of association with a more oceanic biofacies is the presence of a juvenile isograptid from Hodgson How Quarry, but this cannot be taken as diagnostic and *Azygograptus* and isograptids are generally not associated in the Lake District.

Lithofacies association. *Azygograptus* occurs mainly in three different lithofacies: (1) flaggy sandstone facies (cf. Beckly 1987); (2) turbidite sandstone beds interbedded with siltstone; (3) massive siltstone or mudstone.



TEXT-FIG. 2. Graptolite distribution within the Tøyen Shale Formation of Oslo. Lithological column after Erdtmann (1965).



TEXT-FIG. 3. British *Azygograptus*-yielding localities. A, Lake District: A1, Robinson Mountain, Buttermere, scree SW of Robinson Crags (NY 210170); A2, scree approximately 50 m N of Cairn at 703 m on ridge between Hopegill Head and Whiteside (NY 17822225); A3, large scree, 970 m SSE of summit of Swinside, Lorton, (locality 1046 of Jackson (1962)) (NY 179233); A4, Hodgson How Quarry, near Portinscale (NY 24372362); A5, road-cutting 466 m SW of summit of Seat How, Thornwaite (locality 1032 of Jackson (1962)) (NY 210253); A6, Barf, near Basenthwaite Lake (NY 217267); A7, Carlside Edge, Skiddaw (NY 254278); A8, 160 m at 160° from summit of Ling Fell (NY 18012844); A9, scree approximately 50 m N of cairn at 703 m on ridge between Hopegill Head and Whiteside (NY 17822225); A10, Tom Rudd Beck west of Ling Fell, 100 m SW of Beckhouse

The flaggy sandstone facies comprises thinly interbedded and interlaminated fine sandstone and siltstone. The sandstone laminae are often lenticular and show ripple cross-lamination, whilst bioturbation is moderately abundant but is predominantly parallel to bedding. This is the typical facies in which *Azygograptus* is found in North Wales and generally occurs between an underlying cross-bedded sandstone unit and overlying parallel laminated siltstone (see Text-fig. 1). This, and the nature of the facies suggest deposition in a shelf setting, probably below normal wave base (Beckly 1987).

The other two lithofacies generally suggest a deeper water depositional environment, with the exception of the silty mudstone in which *Azygograptus* occurs in the Aberdaron Area. This is comparable to the flaggy sandstone facies in both its stratigraphic position and associated biofacies, and is thought to have been deposited in a similar environment which was starved of coarser clastic material (Beckly 1987).

The shales in which *Azygograptus* occurs in Scandinavia, are predominantly dark in colour, and sandstone is generally absent. In the Tøyen Shale Formation (Text-fig. 2), *A. eivionicus* occurs in the slightly paler, greenish, Slemmestad Member, and the occurrences of *A. suecicus* in Scania are in yellowish-green shale.

Though much of the material from the Lake District is derived from screes, an indication of the lithofacies is provided by the slabs on which the specimens occur, and *Azygograptus* is predominantly associated with sandier lithologies, and not massive mudstone. Since graptolites are preserved on siltstone slabs the association is not a function of the less penetrative deformation in sandy lithologies. In-situ occurrences further support this with the appearance of *Azygograptus* locally associated with the incoming of sandy beds and laminae (A. W. A. Rushton pers. comm.). The two populations collected from Hodgson How Quarry both occur in parallel laminated, micaceous, fine sandstone, whilst the interbedded mudstone is virtually barren of graptolites.

The significance of the association with turbidite beds is less clear because the amount of fragmentation appears inadequate for the material to have been transported by a turbulent flow. Alternative explanations are:

1. *Azygograptus* was carried into the area of deposition by processes affecting the higher part of the water column which have a functional relationship to the turbidite flows, but this still fails to explain the absence of other graptolites.

2. Rapid burial by the sandstone beds allowed preservation on an oxic sea-floor, in an environment not favoured by other graptolites.

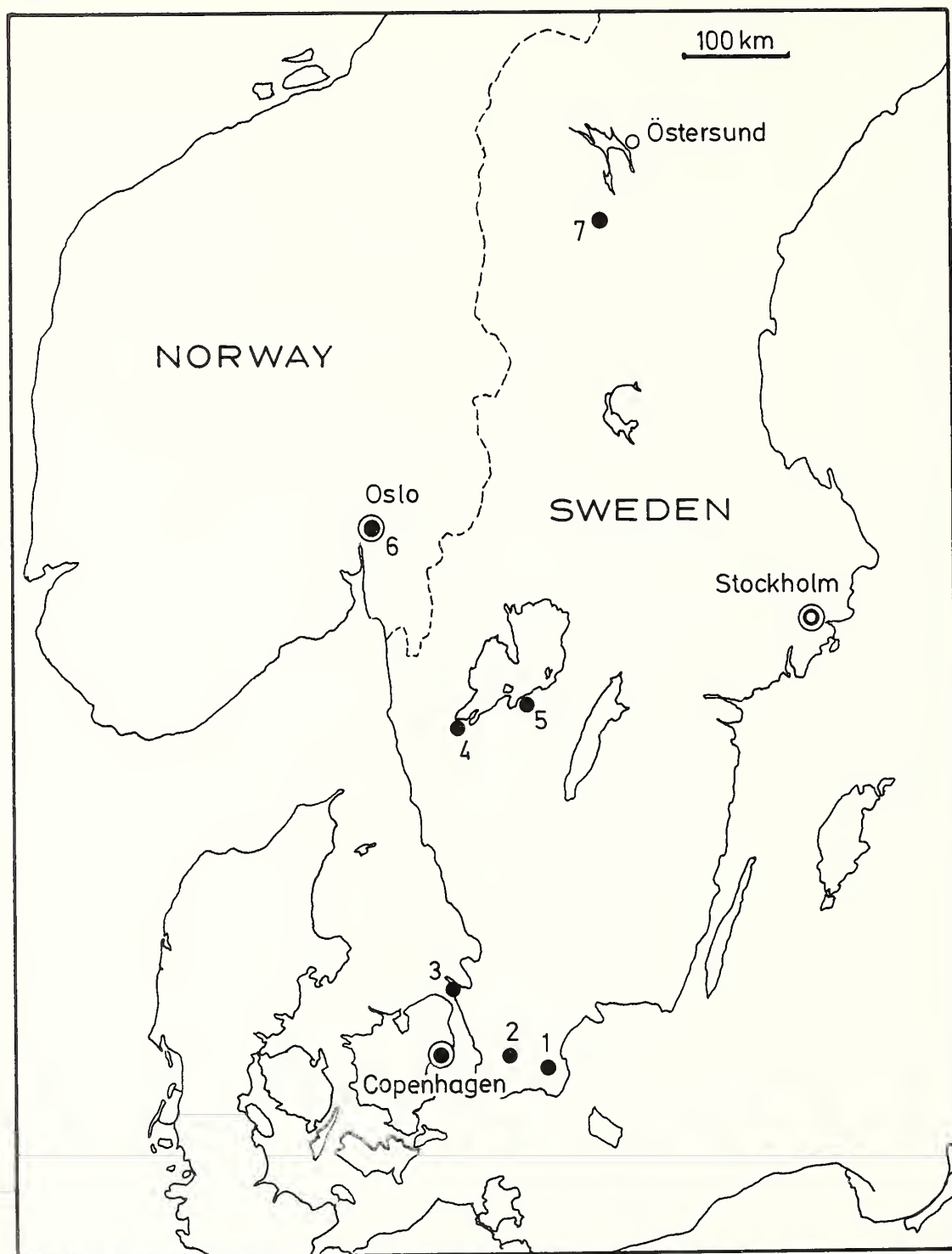
3. The turbidite beds reflect a change to an environment which *Azygograptus* favoured, e.g. increased turbidity of the water.

The common factor in all these explanations is a change in habitat to one which was favoured by *Azygograptus*, and the low diversity of many associated faunas suggests the change was disadvantageous to most other graptolite species.

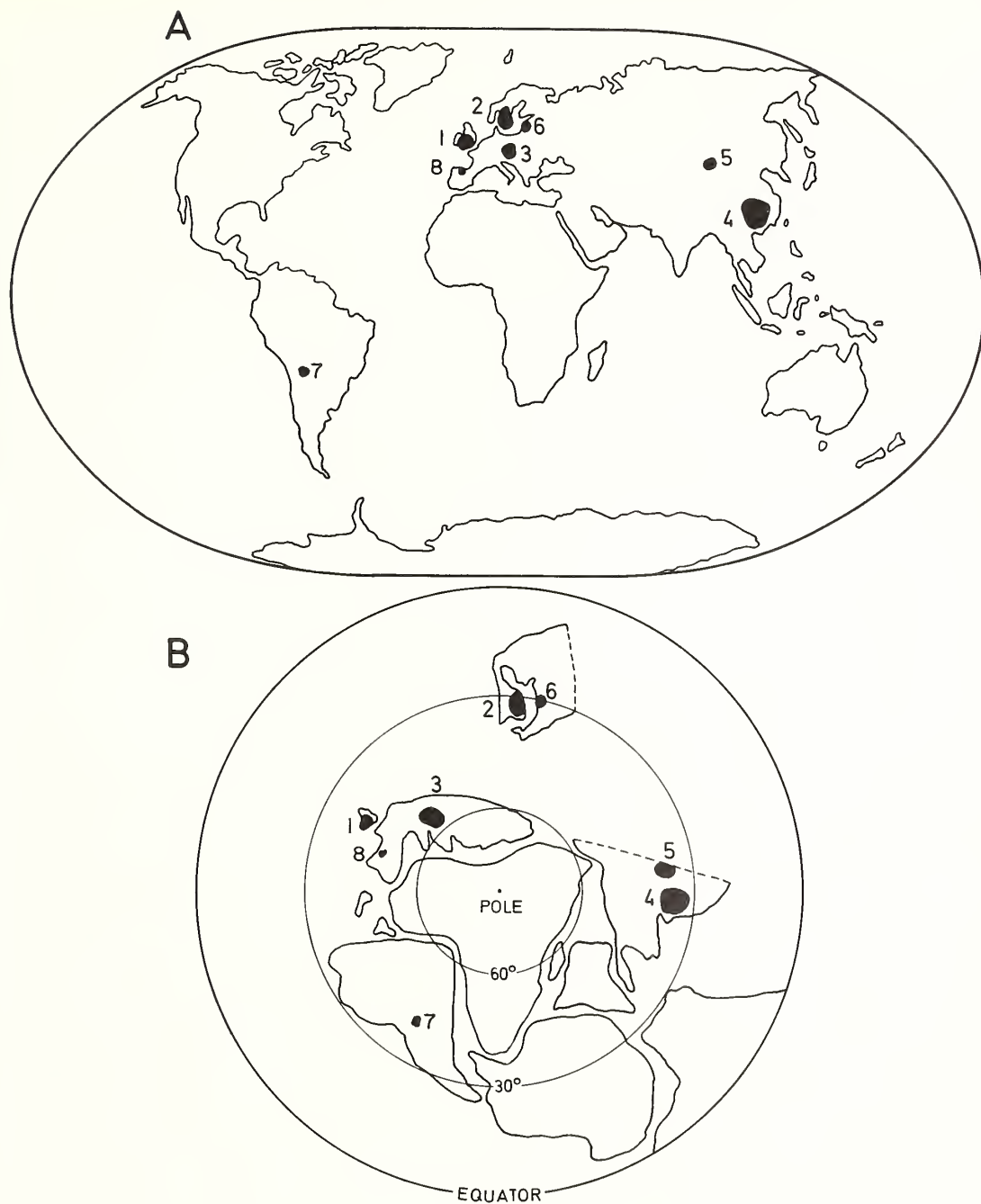
Geographical distribution

The *Azygograptus* yielding localities of Britain and Scandinavia are shown in Text-figures 3 and 4 respectively, whilst the global distribution is shown in Text-figure 5. When plotted on the same palaeogeographic reconstruction, *Azygograptus* shows a very similar distribution to the trilobite genus *Neseuretus* (cf. Fortey and Morris 1982, fig. 2). The major difference is that *Azygograptus* is not restricted to Gondwana but extends into Baltica. However, all occurrences lie above 30° latitude, and a high latitude position is now thought to characterize the Atlantic graptolite province.

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- Cottage (NY 16382898). B, North Wales: B1, Maen Gwenonwy (SH 20052596); B2, Rhiw (SH 22322847); B3, Bryn croes (SH 23173150); B4, Nant (SH 297293); B5, Penrhyn Dû (SH 31742653); B6, Castlemarch Farm (SH 31452980); B7, Penrhyndeudraeth (SH 616401); B8, scree on northern slopes of Moel Llynant, Arenig (SH 80793616); B9, above Hafotty Ffilltirgerig, Arenig (SH 81613960); B10, Bangor (SH585731 and SH 591726).
 C, South Wales: C1, Afon Ffynnant (SN 510198); C2, Whitesand Bay (SM 732274).



TEXT-FIG. 4. Scandinavian *Azygograptus* yielding localities. 1, Flagabro-Killeröd, Scania; 2, Fagelsang Boring, Scania; 3, Krapperup Boring, Scania; 4, Hunneberg Mountain, Västergötland (2 localities, Diabasbrottet (Mossebo of Törnquist 1901) and Mossebo (Maletz 1987)); 5, Kinnekulle, Västergötland (see Skoglund 1961); 6, Oslo Region (includes Slemmestad, Tøyen Underground Station); 7, Nipan, Jemtland.



TEXT-FIG. 5. Global distribution of *Azygograptus*. A, Present day geography. B, Lower Ordovician reconstruction (after Fortey and Morris 1982). 1, British occurrences (see Text-fig. 3) and SE Ireland (Brenchley and Harper 1967); 2, Scandinavia (see Text-fig. 4); 3, Bohemia (Bouček 1973); 4, SW China (Mu *et al.* 1979); 5, Gorny Altai (Obut and Sennikov 1984); 6, Middle East Baltic Area (Ulst 1976, pp. 214–221; Paškevičius 1976, p. 135); 7, near Tarija, southern Bolivia (new material); 8, Cantabria, northern Spain (Gutierrez Marco and Rodrigues 1987).

Ecology of *Azygograptus*

In both bio- and lithofacies associations, differences exist between the Scandinavian and British representatives of the genus. However, this may be largely explained by the predominance of *A. lapworthi* and *A. eivionicus* in Britain, compared to their virtual absence from Scandinavia. The facies association and position within the succession of *Azygograptus* in North Wales support the shoreward distribution advocated by Fortey and Owens (1987) but an epiplanktonic mode of life should result in the presence of *Azygograptus* in all graptolite faunas of the Atlantic province. This is not observed and therefore appears to be fairly good evidence that at least some species of *Azygograptus* favoured a shoreward environment.

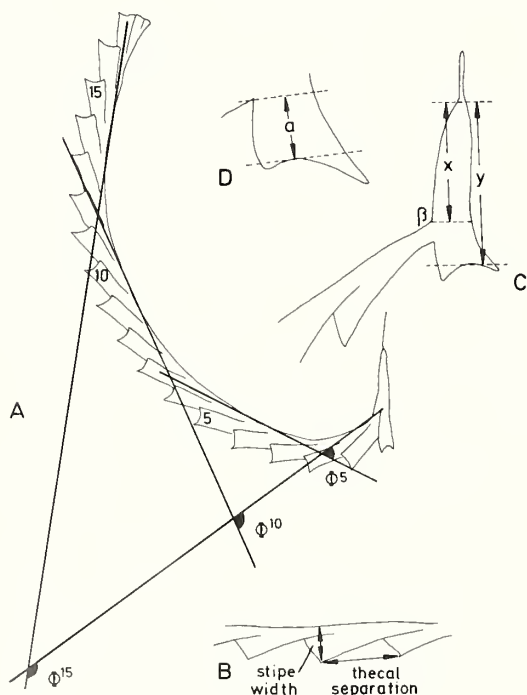
The distribution of extensiforms similar to *D. simulans* is comparable to that of *Azygograptus* and both groups develop synrhabdosomes (Zalasiewicz 1984), suggesting these are also a feature with functional significance to the particular environment. Though the function of synrhabdosomes is uncertain, Zalasiewicz (1984) suggested they maximized breeding in temporary, highly favourable, conditions, implying an *r*-selective environment. Adaptation to an unstable environment may also, at least in part, explain the association of *Azygograptus* with sandstone beds in the Lake District.

At Barf (Locality A6 of Text-fig. 3), *D. simulans* is associated with *A. ellesi*, a species more common in Scandinavia. However the Scandinavian occurrences, with the possible exception of *A. suecicus*, do not display significant differences in distribution to the majority of other graptolites. This may be a consequence of the different palaeogeographic position of Baltica (see Text-fig. 5B).

SYSTEMATIC PALAEOLOGY

Parameters used in descriptions. The measurements used in descriptions are summarized in Text-figure 6:

1. Basal free length of sicula (A on Text-fig. 6D). The distance along a line parallel to the dorsal sicula margin, between the aperture and the final point of contact of the first theca.
2. Stipe Divergence Angle (β on Text-fig. 6C). Angle between dorsal wall of sicula and dorsal wall of proximal part of stipe.



TEXT-FIG. 6. Parameters used in descriptions. A, entire rhabdosome; Φ^5 , Φ^{10} , Φ^{15} , stipe rotation by each of these thecae. B, stipe detail showing stipe width and thecal separation. C, sicula: x, distance to origin of th.1¹; y, sicular length; β , stipe divergence angle. D, detail of sicular aperture: a, basal free length.

3. Origin of th 1¹ is given as a fraction of the length of the sicula measured away from the apex (x/y on Text-fig. 6c).
4. Thecal Separation/Density. Thecal density is given as a recalculated value in thecae/10 mm, based on measurements of thecal separation: the distance between successive thecal apertures (see Text-fig. 6b).
5. Stipe curvature: Quantified as the degrees of rotation between lines tangential to the proximal and distal dorsal stipe margin, measured at th 5, th 10, th 15 etc. (see Text-fig. 6A).

Repositories of material mentioned. The following abbreviations are used to indicate where material mentioned is lodged: BU, University Museum, Birmingham; BGS, British Geological Survey, Keyworth; BM, British Museum (Natural History), London; IC, Imperial College, London (teaching collection); LO, Palaeontological Institute, University of Lund; NMW, National Museum of Wales, Cardiff; PMO, Paleontologisk Museum, Oslo; SGU, Sveriges Geologiska Undersökning, Uppsala; SM, Sedgwick Museum, Cambridge; TUB, Technische Universität Berlin.

Order GRAPTOLOIDEA Lapworth, 1875
Family DICHOGRAPTIDAE Lapworth, 1873
Subfamily AZYGOGRAPTINAE Mu, 1950

Diagnosis. Dichograptids with single stipe originating from th 1¹. The sicula bears two processes on aperture.

Discussion. Mu (1950) erected a monotypic family Azygograptidae containing *Azygograptus*, but since then a number of other genera have been established for single-stiped species: *Nicholsonograptus* Bouček and Přibyl, 1953, *Parazygograptus* Kozłowski, 1954, *Pseudazygograptus* Mu, Lee and Geh, 1960, *Hemiholmograptus* Hsu and Chao, 1976, and *Jishougraptus* Geh, 1988.

In all these genera the stipe is formed by th 1¹, except for *Parazygograptus* in which the stipe is based on th 1² and is pendent. This genus is founded on a single isolated specimen of the type species *P. erraticus* Kozłowski. In other respects this specimen is very similar to the co-occurring pendent *Didymograptus rozkowskiae* Kozłowski and could therefore represent a broken rhabdosome. For this reason, *Parazygograptus* is tentatively regarded as a junior synonym of *Didymograptus*.

Nicholsonograptus was included within the Sinograptidae by Skevington (1966), Bulman (1970) and Bouček (1973). Wang (1975) placed *Nicholsonograptus* in his new family Paradidymograptidae though the necessity for this family is questionable. *Hemiholmograptus* is now regarded as a junior synonym of *Nicholsonograptus* (Geh 1988). *Pseudazygograptus* Mu *et al.*, 1960, with *A. incurvus* as the type species, was referred to the Virgellina by Fortey and Cooper (1986) on account of the prominent virgellar structure illustrated by Finney (1980). However, this structure seems to be an extended growth of the rutellum rather than a virgellar spine and inclusion of *Pseudazygograptus* within the Dichograptidae is therefore preferred.

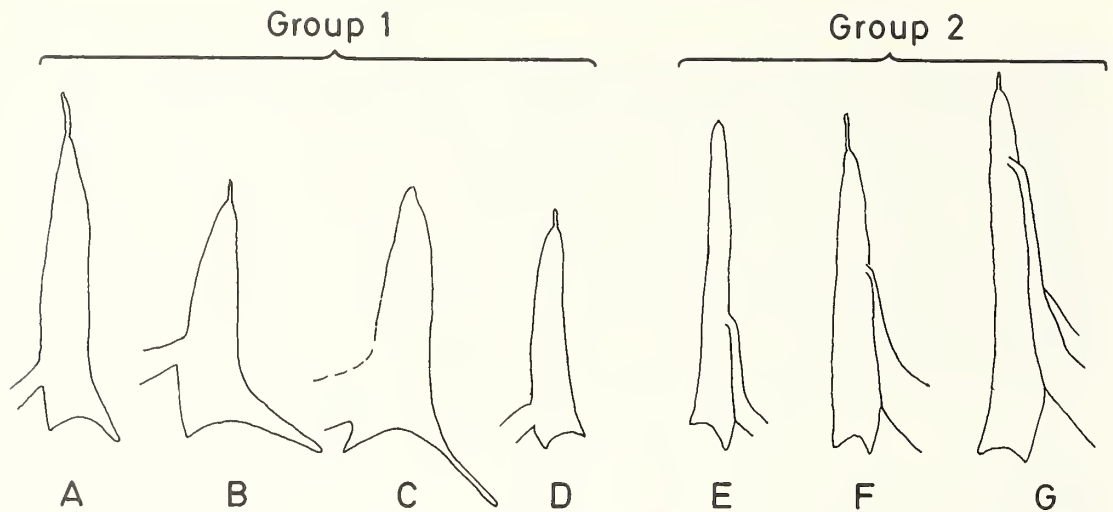
Genus AZYGOGRAPTUS Nicholson and Lapworth, *in* Nicholson, 1875

Type species. *Azygograptus lapworthii* Nicholson, 1875.

Diagnosis. Rhabdosome of single, uniserial, declined stipe originating from th 1¹. Stipe either straight or curved (causing stipe to be reclined in distal part). Thecae simple, elongate, conical and inclined at low angle to the dorsal margin.

Discussion. Elles and Wood (1902, p. 93) recognized three informal groupings of *Azygograptus* which Obut and Sennikov (1984) elevated to subgenera: *A. (Azygograptus)*, *A. (Eoazygograptus)*, and *A. (Metazygograptus)*. One of the main characters on which these groups were based was the origin of th 1¹ and its growth relative to the sicula. Only two groups are recognized reliably by the present study on the presence or absence of adpressed growth of th 1¹ and the sicula (see Text-fig. 7). However, the named subgenera have not been used because of difficulties with the type species.

The type species of the subgenus *Metazygograptus* is *A. suecicus* but the characters of the Elles



TEXT-FIG. 7. Groupings of *Azygograptus* on proximal development (all $\times 20$). Group 1 – lacking adpressed growth of th 1¹. Group 2 – with adpressed growth of th 1¹. Species illustrated are: A, *A. eivionicus*; B, *A. lapworthi*; C, *A. hicksii*; D, *A. suecicus*; E, *A. ellesi*; F, *A. minutus*; G, *A. validus*.

and Wood grouping (1902) were based on material from Barf, now thought to be *A. ellesi*. As a result *A. (Metazygograptus)* is a subjective junior synonym of *A. (Azygograptus)* which is characterized by the absence of adpressed growth on th 1¹ and the sicula.

The type species of *A. (Eozygograptus)* is *A. coelebs* but no specimens adequate to confirm the character of this species have been found. The published descriptions (Elles and Wood 1902) would indicate placement in Group 2 (see Text-fig. 7), but until this can be confirmed the use of the subgenus is unsupported.

Azygograptus lapworthi Nicholson, 1875.

Pl. 1, fig. 2; Text-figs 10A–O, 11 A–E, 12

1875 *Azygograptus lapworthi* Nicholson, p. 270, pl. 7, fig. 2–2c.

1898 *Azygograptus lapworthi* Nicholson; Elles, p. 513.

EXPLANATION OF PLATE 1

Figs 1 and 11. *Azygograptus ellesi* Monsen. 1, SGU 7554; Nipan, Jemtland, $\times 10$. 11, PMO 118.576; 16.25–16.42 m interval of Toyen Section, Oslo, $\times 20$.

Fig. 2. *Azygograptus lapworthi* Nicholson. SM A55166a; Castlemarch Farm, North Wales, $\times 20$.

Figs 3, 4, 7, 8. *Azygograptus eivionicus* Elles. 3, NMW 85.16G.94; Garth Point, Bangor, North Wales, $\times 15$. 4, 7, 8, Rhiw, North Wales; 4, BM Q5884, $\times 15$; 7, BM Q5896, $\times 20$; 8, SM A22601, $\times 10$.

Fig. 5. *Azygograptus suecicus* Moberg. SGU 7895; Killeröd, Scania, $\times 8$.

Figs 6, 9, 10. *Jishougraptus novus* sp. nov. Paratypes; from 16.15–16.25 m interval of Toyen Section, Oslo, $\times 20$. 6, PMO 118.582–3. 9, PMO 118.593. 10, PMO 118.588.

Figs 7 and 8. *Azygograptus eivionicus* Elles. Rhiw, North Wales. 7, BM Q5896, $\times 20$. 8, SM A22601, $\times 20$.

Figs. 11. *Azygograptus ellesi* Monsen. PMO 118.576; 16.25–16.42 m interval of Toyen Section, Oslo, $\times 20$.

Fig. 12. *Azygograptus minutus* sp. nov. SGU 7556 [paratype]; Diabasbrottet Section at 7.09 m level, Hunneberg Mountain, Västergötland, Sweden, $\times 20$.

Fig. 13. *Azygograptus validus* Törnquist. SGU 7557; Diabasbrottet Section at 4.74 m level. Hunneberg Mountain, Västergötland, Sweden, $\times 15$.



BECKLY and MALETZ, *Azygograptus*, *Jishougraptus*

- 1902 *Azygograptus lapworthi* Nicholson; Elles and Wood, p. 93, text-fig. 54; pl. 13, fig. 1a-b.
 1915 *Azygograptus lapworthi* Nicholson; Nicholas, pp. 112, 121.
 1938 *Azygograptus eivionicus* Elles; Matley, p. 559.
 1943 *Azygograptus lapworthi* Nicholson; Fearnside and Davies, p. 253.
 ?1979 *Azygograptus lapworthi* Nicholson; Mu *et al.*, pp. 109–110, pl. 38, figs 3–7.
 1984 *Azygograptus lapworthi* Nicholson; Zalasiewicz, p. 427, fig. 2e-f.
 1988 *Azygograptus lapworthi* Nicholson; Beckly, p. 325.

Diagnosis. *Azygograptus* with no adpressed growth of th 1¹ and sicula and basal free length of the sicula commonly exceeding 0.2 mm. Prominent rutellum on sicular aperture in some populations.

Type material. The original slab figured by Nicholson from Dover's collection has not been traced. Differing populations of *Azygograptus* are certainly present at the type locality, and there is no clear evidence on the level from which the original material came. A considerable amount of material from Hodgson How is present in many museum collections and the original slab may be amongst this.

Type locality. Hodgson How Quarry, Keswick, English Lake District (National Grid Reference NY 243236). The succession comprises turbidite sandstone beds, some over 30 cm thick, interbedded with siltstone. Two *Azygograptus* populations have been recovered during this study; one close to the base of the exposed section and the other about 20 m above, both from parallel laminated, micaceous sandstone. These populations show quite marked differences (see Text-figs 9 and 10) and further variations shown by some museum material suggest at least a third population. The lower of the *in situ* populations is sufficiently different to the original description to suggest it is unlikely to be topotype (see discussion).

Jackson (1962) claimed the fauna from Hodgson How Quarry indicated the *nitidus* biozone, whilst Eastwood *et al.* (1968) claimed the assemblage was indicative of the *Dichograptus* biozone, a subdivision rejected by Jackson (1962). Material collected during this study, which includes *D. hirundo* and a juvenile '*Isograptus*', indicates a higher horizon and probably the *gibberulus* biozone. Lower *in situ* population: BM Q5630–Q5631. Higher *in situ* population: BM Q5108–Q5117.

Other occurrences.

1. Carlside Edge (locality A7 of Text-fig. 3). A poorly preserved fauna in micaceous grey siltstone. BM P7211–P7212, P7218.
2. Castlemarch Farm, North Wales (SH 31452980) (locality B6 of Text-fig. 3). Sparse fauna, occasionally preserved in partial relief. Only faunal element known. SM A55166; NMW 85.16G. 73–74.
3. Penrhyn Dû (locality B5 of Text-fig. 3); 1.5 km south-southeast of Abersoch (NGR SH 31742653) (Localities η_3 and η_4 of Nicholas 1915, pl. 13). Material comes from the 'Transition Beds' between the St Tudwal's Sandstone and Llanengan Mudstone (cf. Nicholas 1915). The lithofacies is typical of the 'flaggy sandstone facies' and the population forms a monospecific assemblage. NMW 85. 16G. 122–124.
4. Small Valley 400 m west of Bryncroes (SH 23173150) (locality B3 of Text-fig. 3) Abundant population forming monospecific assemblage in 'flaggy' sandstone facies of Sarn Formation (Beckly 1988). BM Q5876–Q5879.
5. Abandoned mine workings just north of Penrhyndeudraeth (SH 616401) (locality B7 of Text-fig. 3). Termed Pant-y-wrach Beds by Fearnside and Davies (1943), who mention a fauna comprising *A. lapworthi* and *Phyllograptus angustifolius*. Only specimens of *A. lapworthi* have been examined and these occur in parallel laminated coarse siltstone. All specimens have been collected from the spoil of the mine workings. NMW 85.16G.121; BGS Z1672; IC 1514.
6. Near Tarija, southern Bolivia. Few specimens as monospecific assemblage, preserved as silvery periderm in grey silty mudstone. The succession comprises 4,500 m of shale with few sedimentary structures, and all other graptolites found indicate a lower to middle Arenig age, TUB BOL 387P 01–05.

Description. Sicula 1.0–1.5 mm long and 0.2–0.35 mm wide at aperture excluding ventral lip (see Text-fig. 8). Stipe originates at about 0.7 of sicular length and diverges immediately at an angle of about 135–140°. Prominent basal free length to sicula up to 0.45 mm long and often greater than 0.2 mm.

Stipe moderately flexed with rotation by th 5 between 15° and 30° but ranging up to 55° by th 10 or th 15. Rhabdosomes up to 30 mm long observed but 50 mm has been claimed (Elles 1898). Initial stipe width at first theca about 0.5 mm or less but rapidly increases to fairly constant width 0.8–1.05 mm. Maximum widths in

Hodgson How Quarry (lower Population)

Hodgson How Quarry (*A. lapworthi*)

Hodgson How Quarry [GSM 46365]



Castlemarch Farm



Bryncroes



Penrhyn Dû



Penrhyndeudraeth



sicular apertures x20

basal free length of sicula

TEXT-FIG. 8. Sicular apertures and basal free length histograms for different populations of *Azygograptus lapworthi*.

excess of 1 mm are more characteristic of longer stipes and may indicate a slow distal stipe expansion. Thecal spacing 1.2–1.6 mm; thecal density 6–9 th/10 mm; thecal inclination 10–12°; thecal overlap a little over one-third. Thecal density and overlap generally increase over the first few thecae. One specimen from Penrhyndeudraeth (Text-fig. 10G) has some thecae with apertures isolated by a notch about 0.2 mm deep.

Zalasiewicz (1984) described a synrhabdosome of *A. lapworthi* from Hodgson How. Another possible synrhabdosome has been recognized during this study in the population from Brynccroes (Text-fig. 12). It appears to comprise predominantly juvenile rhabdosomes and is more unidirectional than the example from Hodgson How.

Discussion. The narrower stipe and higher thecal density serve to distinguish *A. lapworthi* from *A. hicksii* (Text-fig. 15), but stipe characters are inadequate to distinguish it from *A. eivionicus*, with only slightly greater stipe width in *A. lapworthi*. Distinction of *A. lapworthi* from *A. eivionicus* is therefore dependent on features of proximal development and in particular the basal free length of the sicula, which in *A. eivionicus* only rarely exceeds 0.2 mm (Text-fig. 9). A more prominent rutellum (see Text-fig. 8) and shorter sicula also distinguish some populations of *A. lapworthi* but these characters are not always developed. *A. suecicus* is distinguished by the absence of a rutellum.

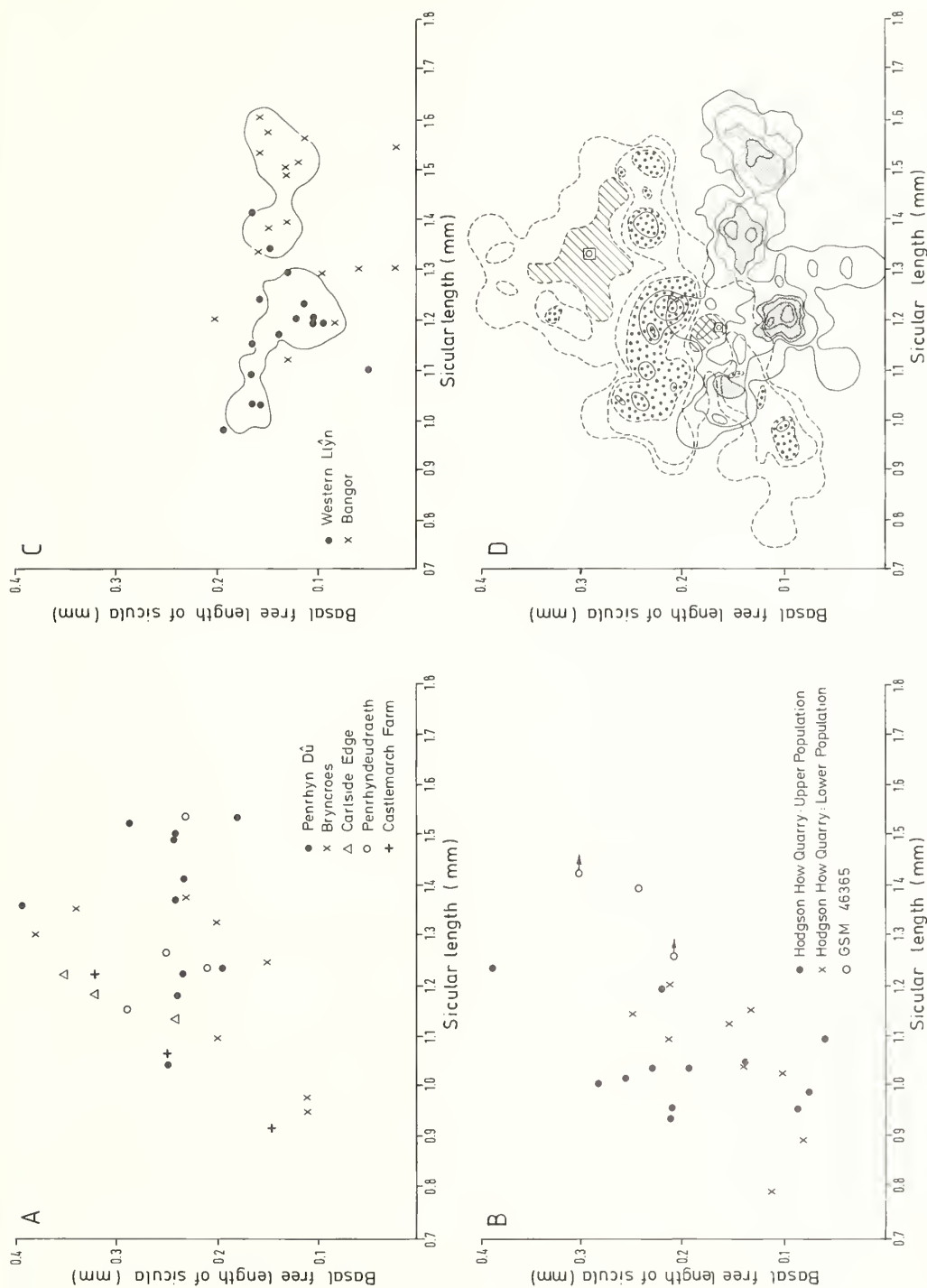
The majority of published descriptions of *A. lapworthi* (Nicholson 1875; Elles 1898; Elles and Wood 1902) have been based on material from the type locality, and therefore synonymy is assumed. Despite this direct comparison, there are quite significant differences in the values quoted, particularly sicular length. The value given by Nicholson (1875) in the original description was 1.05 mm, but Elles (1898) and Elles and Wood (1902) quoted values of 1.26 mm and 1.5 mm respectively.

These differences may be largely explained by the presence of more than one population at the type locality, and that more than one form of the species may exist. The population from the base of the exposed succession in Hodgson How Quarry has lower thecal separation (1.1–1.3 mm) and narrower stipes (0.4–0.5 mm, max. 0.75 mm) than is typical of either *A. eivionicus* or *A. lapworthi*, though the longest only reaches th 7. The sicular characters are a mixture of those seen in *A. eivionicus* and *A. lapworthi* (see Text-fig. 9) with the basal free length ranging above 0.2 mm, though predominantly less, and a sicular length of about 1 mm. The population is more similar to *A. eivionicus* but with some aspects of a transitional form.

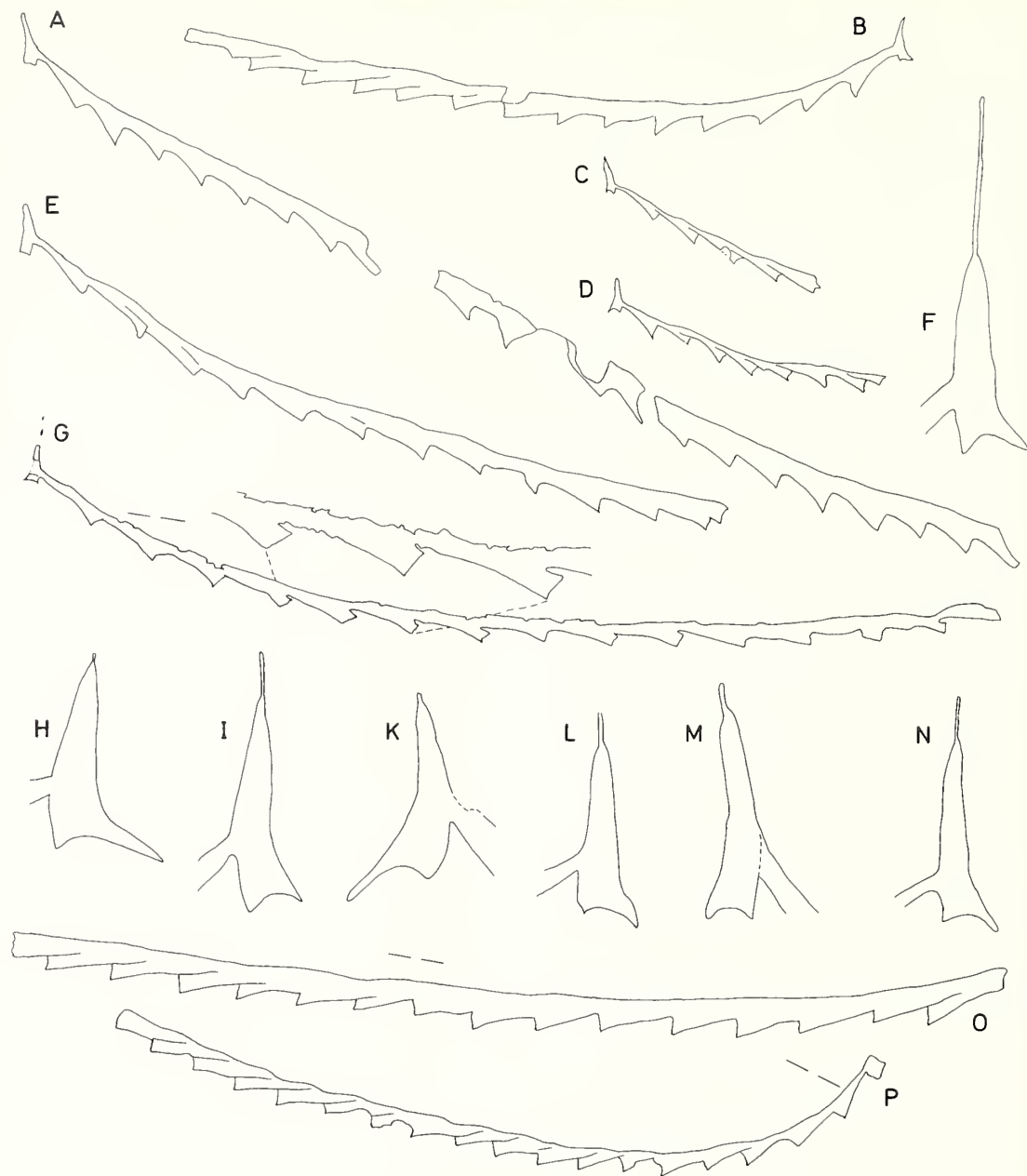
The population from 20 m above is characterized by a short sicula, about 1.0 mm long, significant basal free length to the sicula and a very prominent rutellum (see Text-figs 8 and 9). However, indications of at least a third population are provided by a slab in the BGS collections (GSM 46365) in which the sicular length ranges up to 1.5 mm and there is only slight development of a rutellum, but with a significant basal free length. The specimen is labelled *A. lapworthi* in Nicholson's handwriting.

These differences appear subtle but similar variation is shown by the occurrences in North Wales. Though few specimens are available, the population from Castlemarch Farm shows the prominent rutellum associated with a sicular length of about 1 mm. However the other three North Wales populations lack the prominent rutellum, and have a sicular length ranging up to 1.5 mm. Since both these forms appear to occur at the type locality, either could be the true type-population. The original description is also inadequate to distinguish them, since it combines short sicular length with a poorly developed rutellum. For these reasons the species is broadly defined on the basal free length of the sicula only.

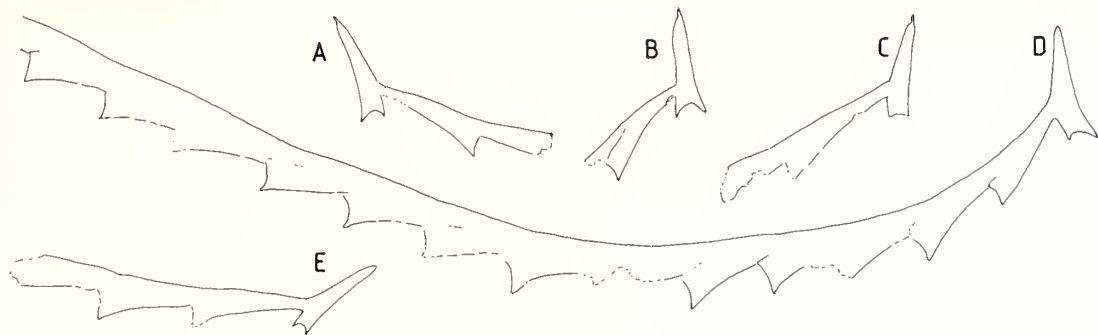
The only confirmed occurrence of *A. lapworthi* from outside Britain is the new material from Bolivia (Text-fig. 11). The basal free length of the sicula clearly places this population in *A. lapworthi* but the stipe width appears to be greater than in the British populations. The material described by Mu *et al.* (1979) from China as *A. lapworthi* may also belong to the species. From translations provided by Chen Xu, they quote a sicular length of 1.6 mm and for which a basal free length of 0.4 mm may be inferred. However, it is unclear from the description whether there is adpressed growth of th 1¹ and the sicula; th 1¹ is described as growing 'downward and outward'.



TEXT-FIG. 9. Cross-plots of sicular basal free length and sicular length for *Azygograptus lapworthi* and *A. evivonicus*. A, *A. lapworthi* populations other than from the type locality. B, *Azygograptus* populations from Hodgson How Quarry (type locality for *A. lapworthi*). C, *A. evivonicus* populations from Western Llŷn and Bangor (areas of densest distribution for each population outlined). D, comparison of density contouring for all the populations of each of the species: *A. evivonicus* contours are shown in solid lines with the areas of densest distribution highlighted in fine stipple; *A. lapworthi* contours are shown in dashed lines with areas of densest distribution highlighted with heavy stipple (internal areas of zero density for *A. lapworthi* are cross-hatched).



TEXT-FIG. 10. *Azygograptus lapworthi* Nicholson. A, B, BM H3365, Hodgson How Quarry, $\times 5$. C, BM Q6331, Hodgson How Quarry, lower population, $\times 5$. D, BM Q6330, Hodgson How Quarry, lower population, $\times 5$. E, BM Q5876, Bryncroes $\times 20$. F, BM Q5877, Bryncroes, $\times 5$. G, BGS Z1672, Penrhyndeudraeth, $\times 5$ (detail $\times 20$). H, BM Q5879, Castlemarch Farm, $\times 20$. I, BM Q5877, Bryncroes, $\times 20$. K, BM Q5110, Hodgson How Quarry, higher population, $\times 20$. L, BM Q6331, Hodgson How Quarry, lower population, $\times 20$. M, NMW 85.16G.124, Penrhyn Dû, $\times 20$. N, IC 1514, Penrhyndeudraeth, $\times 20$. O, NMW 85.16G.123. P, NMW 85.16G.122, different distal stipe morphologies, Penrhyn Dû, $\times 5$.



TEXT-FIG. 11. *Azygograptus lapworthi* Nicholson; from near Tarija, southern Bolivia, $\times 10$. A, TUB BOL387P 01. B, TUB BOL387P 02. C, TUB BOL387P 03. D, TUB BOL387P 04 ($\times 10$). E, TUB BOL387P 05.

Azygograptus hicksii (Hopkinson in Hopkinson and Lapworth, 1875)

Text-fig. 13A–C

- 1875 *Tetragraptus hicksii* Hopkinson in Hopkinson and Lapworth, p. 651, pl. 33, fig. 12a–d.
 1902 *Azygograptus hicksii* (Hopkinson); Elles and Wood, p. 94, text-fig. 55a–b; pl. 13, fig. 2a–e.
 1987 *Azygograptus hicksii* (Hopkinson); Fortey and Owens, p. 275, text-fig. 128b–c.

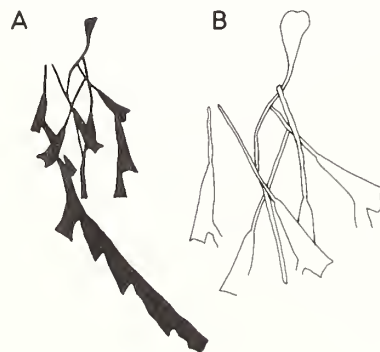
Diagnosis. *Azygograptus* with larger stipe than other species: maximum stipe width 1.0–1.5 mm, thecal density 4–6 th/10 mm. Sicular aperture with elongate rutellum. No adpressed growth of th 1¹ and sicula.

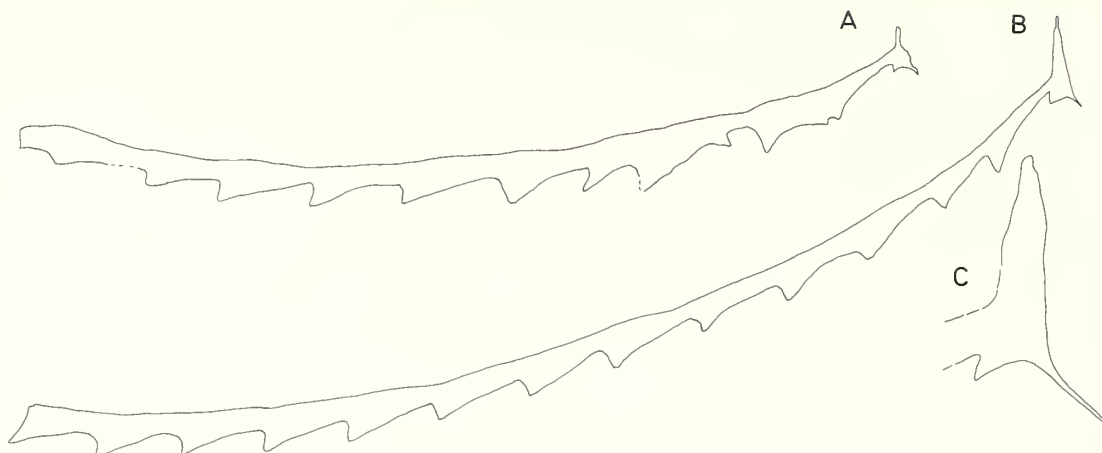
Type material. Lectotype (SM A17381); selected as 'type' by Elles and Wood (1902). All other available specimens (SM A17379–94) are paratypes.

Type locality. Pwlluog, Whitesand Bay, near St David's, Dyfed (SM 732274) (locality C2 of Text-fig. 3). Specimens occur as carbonaceous films in fissile siltstone of Whitlandian age, *Gymnostomix gibbsii* Biozone (Fortey and Owens 1987).

Other occurrences. Afon Ffynnant, east of Carmarthen, South Wales (SN 51061973 to SN 51032003) (locality C1 of Text-fig. 3). Specimens collected from isolated outcrops of shale. Described by Fortey and Owens (1987) and considered transient between *A. eivonicus* and *A. hicksii*. BM Q5172–Q5173.

TEXT-FIG. 12. *Azygograptus lapworthi* Nicholson, BM Q5878, possible synrhabdosome of juvenile rhabdosomes, Bryn-croes; A, $\times 5$; B, $\times 10$.





TEXT-FIG. 13. *Azygograptus hicksii* (Hopkinson); Whitesand Bay, South Wales. A, SM A17392, $\times 5$. B, SM A17933, $\times 5$. C, SM A17933, $\times 20$.

Description. Sicula 1.3–1.5 mm long; 0.4 mm wide at aperture. Prominent rutellum up to 0.5 mm long, on opposite side to stipe. Stipe originates at 0.7–0.8 of sicular length and diverges immediately at an angle of 130–140° leaving a basal free length to the sicula of up to 0.3 mm. Stipe slightly to moderately flexed with 20–30° rotation by th 5 and 40° rotation by th 10. Stipe width at th 1 is about 1 mm (0.8–1.1 mm) and slight expansion gives a distal stipe width of up to 1.5 mm. Thecal separation 1.7–2.7 mm (4–6 th/10 mm) with little variation along the stipe. Thecal inclination about 18°; thecal overlap not visible.

Discussion. The massive form of the stipe and elongate rutellum on sicular aperture make the species readily distinguishable. Fortey and Owens (1987) concluded that the size is unlikely to be the product of deformation. The values given in the above description closely match those given by Fortey and Owens (1987) except for sicular length which they give as reaching 2.1 mm, but no specimens of this length have been observed in the type population during this study.

Apart from the transient population from Afon Ffynnant described by Fortey and Owens (1987), the species has not been recognized other than at the type locality, and therefore on present evidence is restricted to South Wales.

Azygograptus eivionicus Elles, 1922

Plate 1, figs 3, 4, 7, 8; Text-figs 16, 17A–P, 18F–O

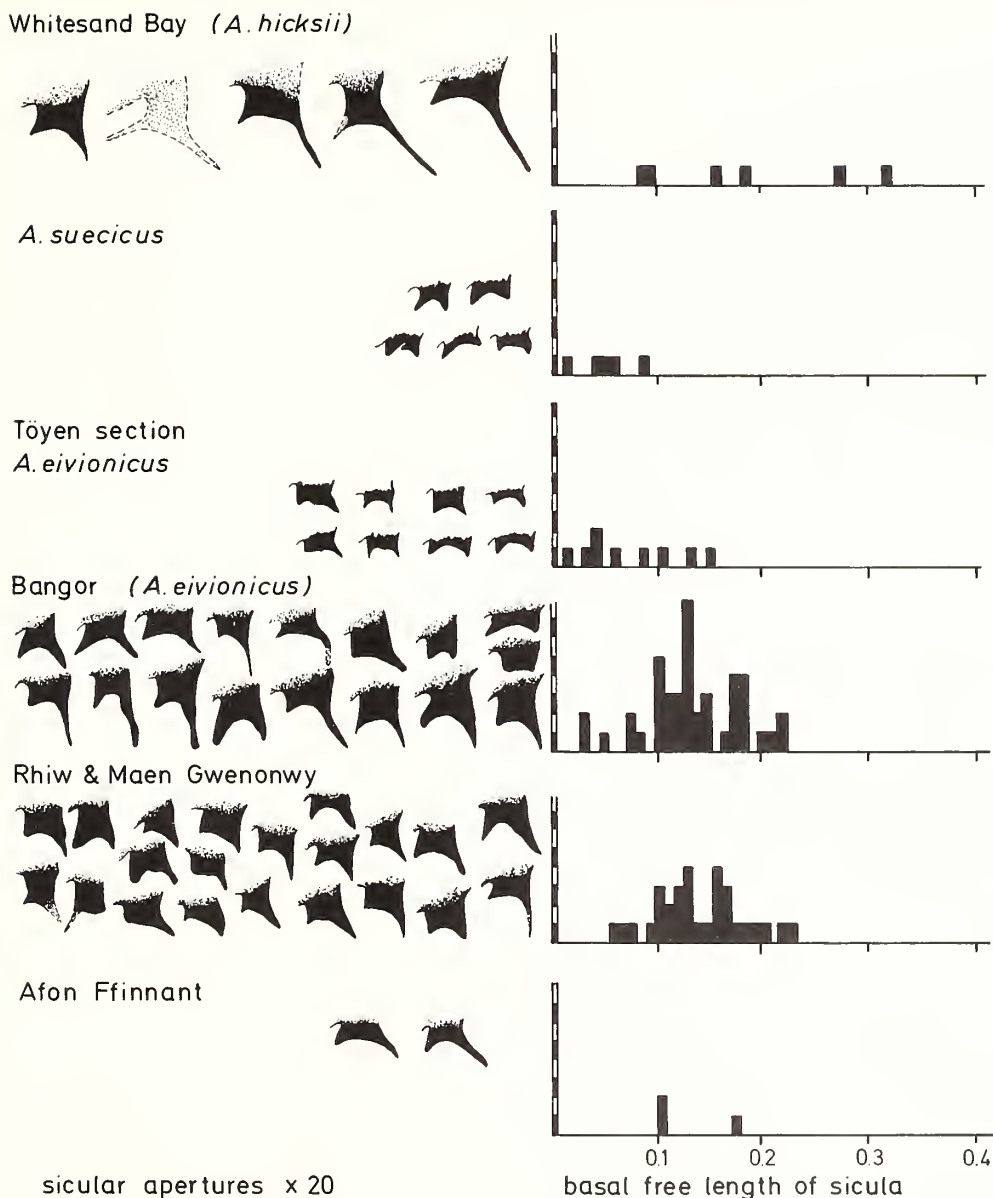
- 1915 *Azygograptus lapworthi* Nicholson; Nicholas, 1915, p. 113.
- 1922 *Azygograptus eivionicus* Elles, p. 299, figs 1–3.
- 1932 *Azygograptus suecicus* Moberg; Matley, p. 261.
- 1987 *Azygograptus eivionicus* Elles; Fortey and Owens, p. 276, figs 128a and 129a–c.

Diagnosis. Basal free length of sicula consistently less than 0.2 mm. Slight to moderate development of rutellum. No adpressed growth of th 1¹ and sicula.

Type material. Holotype, SM A17372; Paratypes, SM A17373–A17374. Strachan (1971, p. 19) listed all these specimens as syntypes, though in the original description a type specimen is clearly designated.

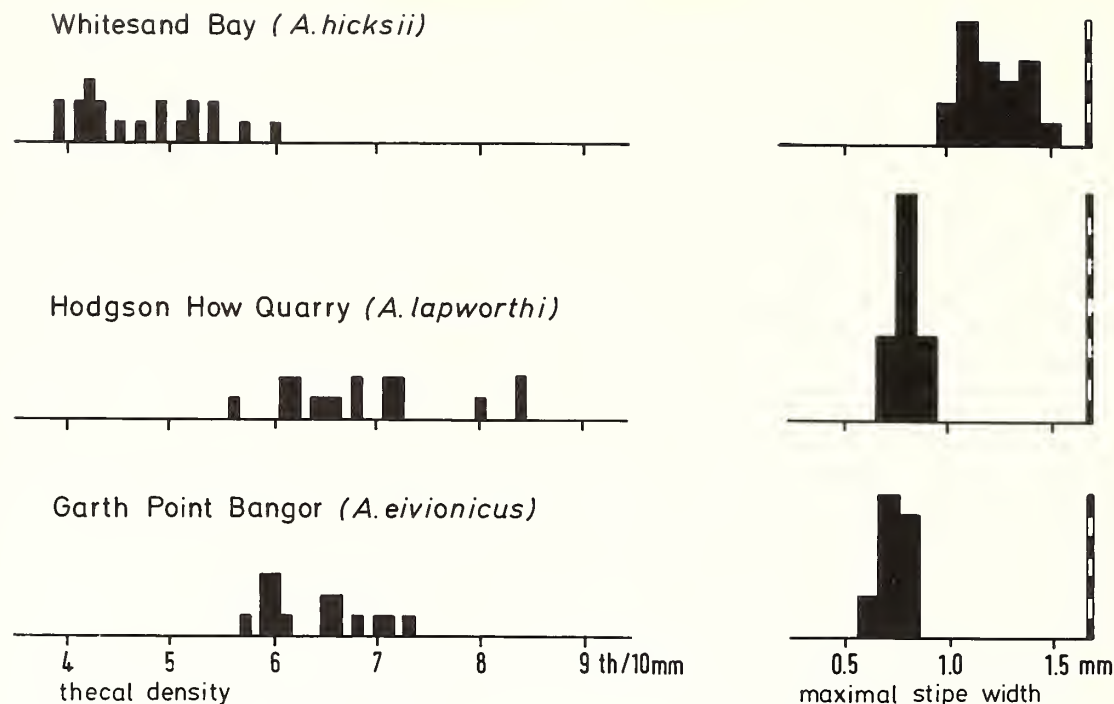
The type material is flattened, matted, fragmentary and strongly deformed. The three specimens figured by Elles (1922) are shown in Text-figure 16 against her original drawings. The differences are most significant in the case of the holotype, for which there is no evidence of the sicula indicated and it is possible that the proximal end is not even reached.

There are very few proximal ends among the material and only one complete sicula (A 17373): 1.1 mm long



TEXT-FIG. 14. Sicular aperture and basal free length in populations of *Azograptus hicksii* (Hopkinson) and *A. eivionicus* Elles.

with a basal free length of 0.08 mm. The basal free lengths in two other measurable siculae are 0.05 and 0.1 mm. None of these are associated with more than a couple of thecae and therefore all may be immature. In figuring A17373, Elles (1922) showed th 1¹ as originating in the mid-part of the sicula and growing adpressed to it for a short distance. There is no evidence for the shoulder this produces and the stipe diverges abruptly at 0.8 of the length. There is a slight inflation of the sicula approximately at its mid-point, but this is also developed on the ventral side and may represent the expansion at the base of the metasicula. The stipe divergence angles measurable on two specimens are 138° and 144° (no correction made for deformation).



TEXT-FIG. 15. Comparison of stipe characters between *Azygograptus lapworthi* Nicholson, *A. eivionicus* Elles and *A. hicksii* (Hopkinson).

Stipe characters are difficult to quantify because of the deformation but are probably most reliable on the holotype which lies almost parallel to the lineation. This has a stipe width of 0.6 mm and a thecal density of 7.4 th/10 mm. Stipes are gently flexed.

Type locality. Valley southeast of Nant, St Tudwal's Peninsula, North Wales (SH 297253), Loc. β of Nicholas (1915, pl. 13), in the Llanengan Mudstone.

Other occurrences.

1. Bangor, North Wales. Two localities on the Bangor foreshore were given in the original description of *A. eivionicus* (Elles 1922): Garth Point (SH 585731) and University College Cliff (SH 59117260). Populations have been collected from two levels at Garth Point (SH 58467320 and SH 58547315), and that from University College Cliff comes from the same part of the succession repeated by faulting. All the populations are very similar and are treated as one. The fauna is monospecific, and occurs in 'flaggy sandstone' of the Maes y Geirchen Sandstone Member of the Nant Ffrancon Formation. The only independent faunal control is an endemic trilobite fauna from the sandstone beds towards the base of the succession (Beckly 1989), and the presence of the Arenig-Llanvirn boundary a few hundred metres above. Material from Bangor Pier: NMW 85-16G-89-99; BM Q5880-Q5883, Q5895. Material from University College Cliff: BM Q5886.

2. Aberdaron Area, Western Llŷn. Populations from Maen Gwenonwy (SH 20052596) (locality B1 of Text-fig. 3) and Rhiw (SH 22322847) (locality B2 of Text-fig. 3) identified as *A. eivionicus* and *A. suecicus* respectively by Elles (*in* Matley, 1932), but now considered to occur in the same stratigraphic unit, the Wig Member of the Aberdaron Formation, and both to be *A. eivionicus* (Beckly 1988). The lithofacies is a massive silty mudstone, and *Azygograptus* along with the trilobite *Merlinia* is very abundant whilst the rest of the fauna is only known from rare specimens and comprises *Hanchungololithus primitivus* (Born), *?Furcolithus*, and *Expansograptus praenuntius* (Törnquist). The fauna is interpreted to come from the lower part of the Arenig succession and to

be overlain by proven Whitlandian and Fennian Faunas. The *Merlinia* is a transient form between *M. selwynii* (Salter) and *M. rhyacos* Fortey and Owens (R. A. Fortey pers. comm.), and this would suggest a late Moridunian to early Whitlandian age (cf. Fortey and Owens 1987). Material from Maen Gwennonwy: NMW 85-16G-100-103; BM Q5885. Material from Rhiw: NMW 85-16G-103-108; BM Q5844, Q5871, Q5875, Q5896-Q5897; SM A22601.

3. Afon Ffinant, South Wales (SN 51032003) (locality C1 of Text-fig. 3). Material described by Fortey and Owens (1987), and occurring as monospecific assemblages in a succession of interbedded turbidite sandstone beds and siltstone. *A. eivonicus* is the lowest graptolite to occur in the succession of the area, and is identified as coming from the *F. radix* biozone at the base of the Whitlandian. BM Q5174-Q5179; NMW 84-17G-105-107.

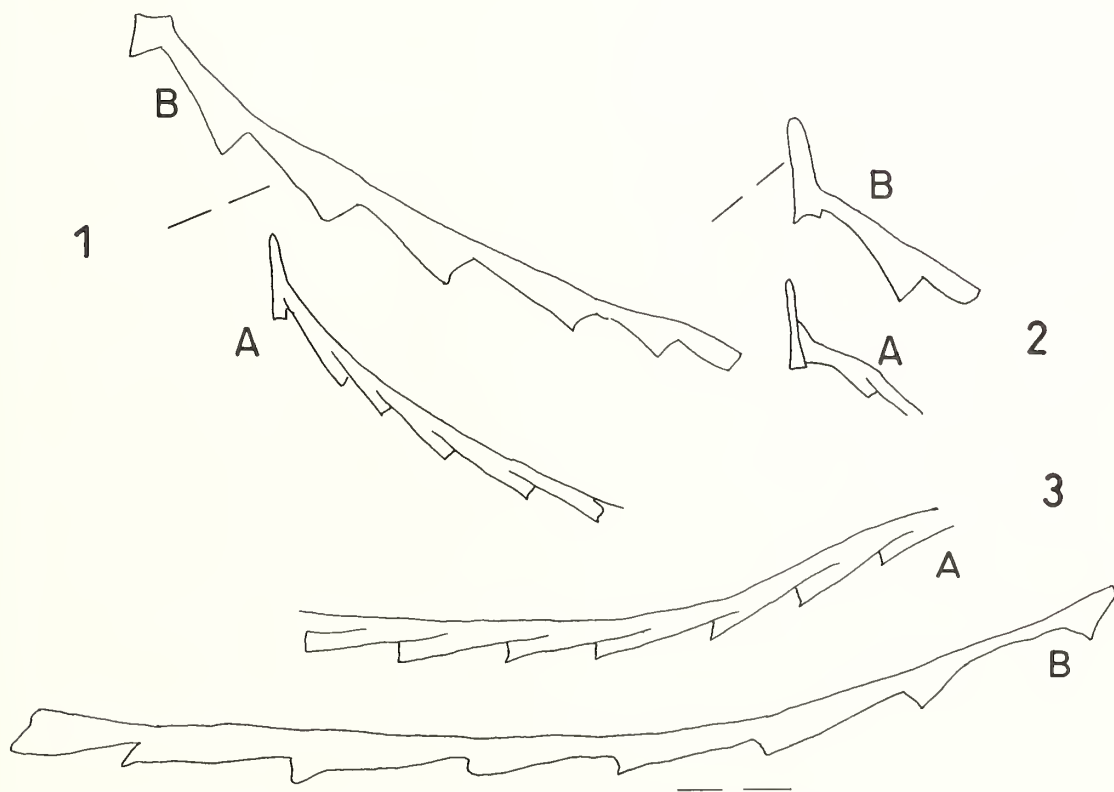
4. Hodgson How Quarry, English Lake District (NY 243236) (locality A4 of Text-fig. 3). Lower *in situ* population discussed under *A. lapworthi*.

5. Tom Rudd Beck, west of Ling Fell, English Lake District (NY 16382898) (locality A10 of Text-fig. 3). Specimens preserved as rusty films in fairly homogeneous dark grey micaceous, fissile siltstone. BGS Rx2207, Rx2210-Rx2211.

6. Ling Fell, English Lake District (NY 18012844) (locality A8 of Text-fig. 3). Specimens preserved as chlorite lined moulds in crenulated mudstone. BGS Rx1691-Rx1692.

7. Toyen Shale, Oslo. Abundant specimens from an interval just below the Orthoceras Limestone between 19.19 and 19.75 m (Text-fig. 2). Graptolite abundance is reduced, compared to the darker lithology of the Galgeberg Member, but the fauna is still diverse and includes *Pseudotrigrionograptus ensiformis*, *Holograptus diffusus*, *Xiphograptus cypselo*, *X. svalbardensis*, *Expansograptus abditus*, *E. distinctus*, *Tetragraptus taraxacum*, and *Dichograptus* sp. PMO 118-601-610.

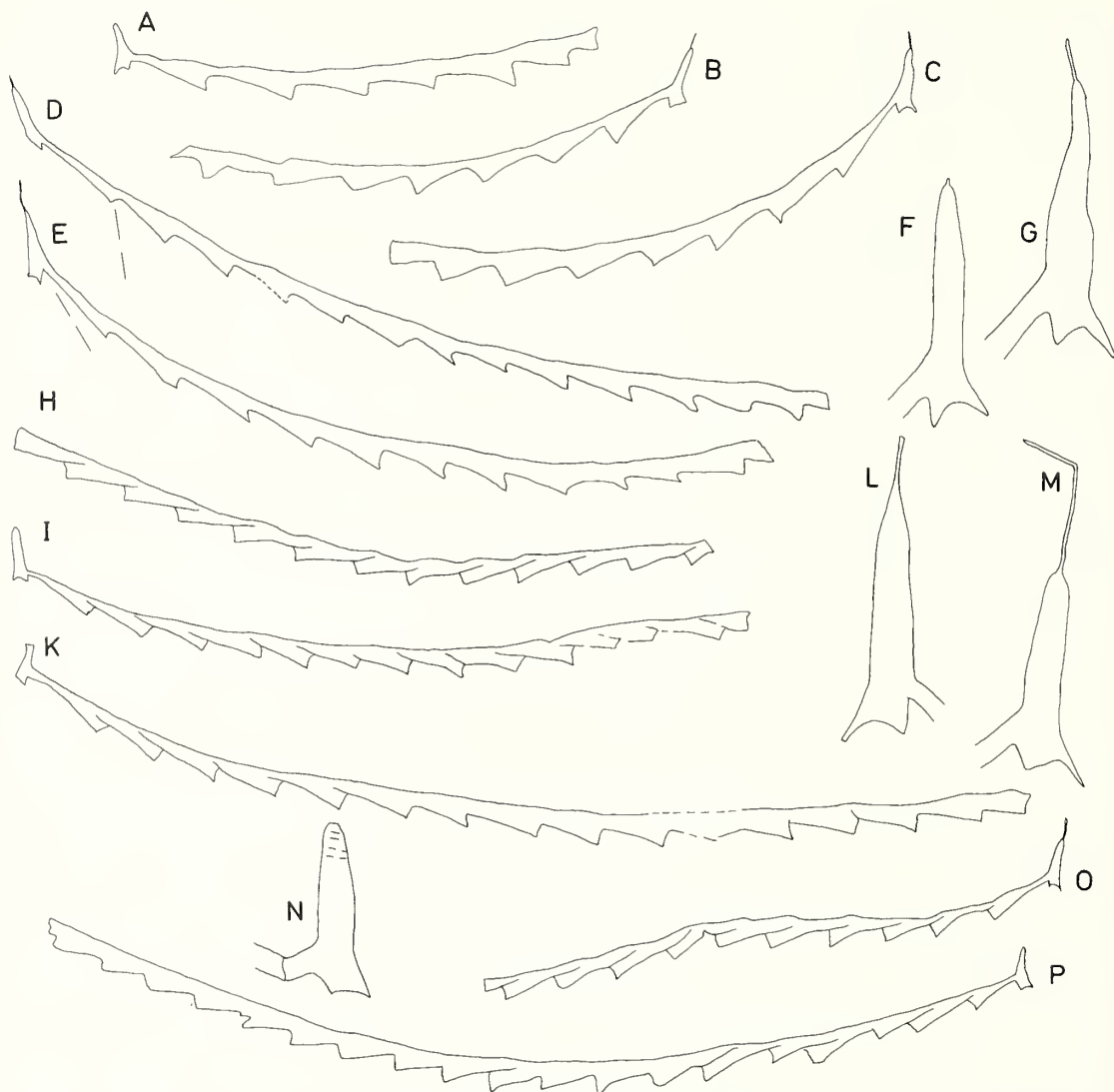
Description. Sicula 1.13-1.62 mm long. Stipe originates at 0.7-0.9 along sicular length and diverges at an angle



TEXT-FIG. 16. Type specimens of *Azygograptus eivonicus* Elles. A, Elles's original drawings (1922) quoted as $\times 5$. B, same specimens redrawn at $\times 10$. 1, SM A17372 (holotype); 2, SM A17377; 3, SM A17374.

between 120° and 160° . Basal free length of sicula 0.1–0.2 mm. Development of rutellum variable but is readily apparent in the majority of specimens. Stipe moderately flexed with up to 50° rotation by th 10 or th 15. Stipe width and thecal separation both vary over the first five thecae. Thecal separation falls from as much as 2.5 mm (4 th/10 mm) to the more typical value of 1.5–1.7 (6–7 th/10 mm); stipe width increases from 0.4–0.6 mm at the aperture of th 1^1 to 0.7–0.8 mm more distally. These changes result mainly from increasing overlap. Thecal inclination $8\text{--}13^{\circ}$. Thecae fairly straight, conical with slight ventral concave curvature. Thecal overlap about two-fifths.

Discussion. Because of the poor preservation of the type material, the population from Garth Point,



TEXT-FIG. 17. *Azyograpthus eivonicus* Elles from North Wales (A–G, Bangor; H–P, Rhiw, Western Llŷn). A, BM Q5881, $\times 5$. B, BM Q5880, $\times 5$. C, BM Q5880, $\times 5$. D, BM Q5883, $\times 5$. E, BM Q5882, $\times 5$. F, BM Q5880, $\times 20$. G, BM Q5880, $\times 20$. H, BM Q5871, $\times 5$. I, BM Q5872, $\times 5$. K, BM Q5874, $\times 5$. L, NMW 85.16G.103, $\times 20$. M, BGS A22601, $\times 20$. N, BM Q5873, $\times 20$. O, BM Q5884, $\times 5$. P, BM Q5875, $\times 5$.

Bangor was selected as the basis for the description because that, and University College Cliff, Bangor, were the only other occurrences accurately located in the original description of the species.

The population from the Aberdaron area is similar to that from Bangor in all characters except sicula length, which is more restricted (1.1–1.4 mm), and in a slightly less pronounced rutellum.

The population from South Wales described by Fortey and Owens (1987) is closely comparable to the populations from North Wales, the only significant difference being the form of the rutellum which is slightly longer and turns away from the aperture more sharply (see Text-fig. 14). The populations from the Lake District are sparse and only the population from Hodgson How Quarry shows significant differences from the North Wales material with more slender stipes and shorter sicula.

The specimens from the Toyen Shale formation are also closely comparable, but with a slightly more slender sicula, and a less prominent basal free length and rutellum (see Text-fig. 14). These features make them similar to *A. suecicus* from which it is distinguished by the presence of a rutellum. The population may be considered transient. Fortey and Owens (1987) suggested specimens described as *A. suecicus* by Mu *et al.* (1979) are *A. eivionicus*, but the description indicates adpressed growth of th 1¹ and sicula and therefore they may be excluded from either of these species.

A. eivionicus is distinguished from *A. hicksii* by its narrower stipe width and smaller thecal separation, and from *A. suecicus* by the presence by a rutellum. Distinction from *A. lapworthi* is more subtle, and is mainly dependent on the basal free length of the sicula which only rarely exceeds 0.2 mm in *A. eivionicus*, and then only slightly (compare Text-figs 9 and 14). Sicula length ranges above that seen in *A. lapworthi*, particularly in the Bangor populations (see Text-fig 9).

Azygograptus suecicus Moberg, 1892

Pl. 1 fig. 5; Text-fig. 18A–E, P

1892 *Azygograptus suecicus* Moberg, p. 342, pl. 8 figs 1 and 2.

1904 *Azygograptus suecicus* Moberg; Törnquist, p. 27, pl. 4 figs 6–11.

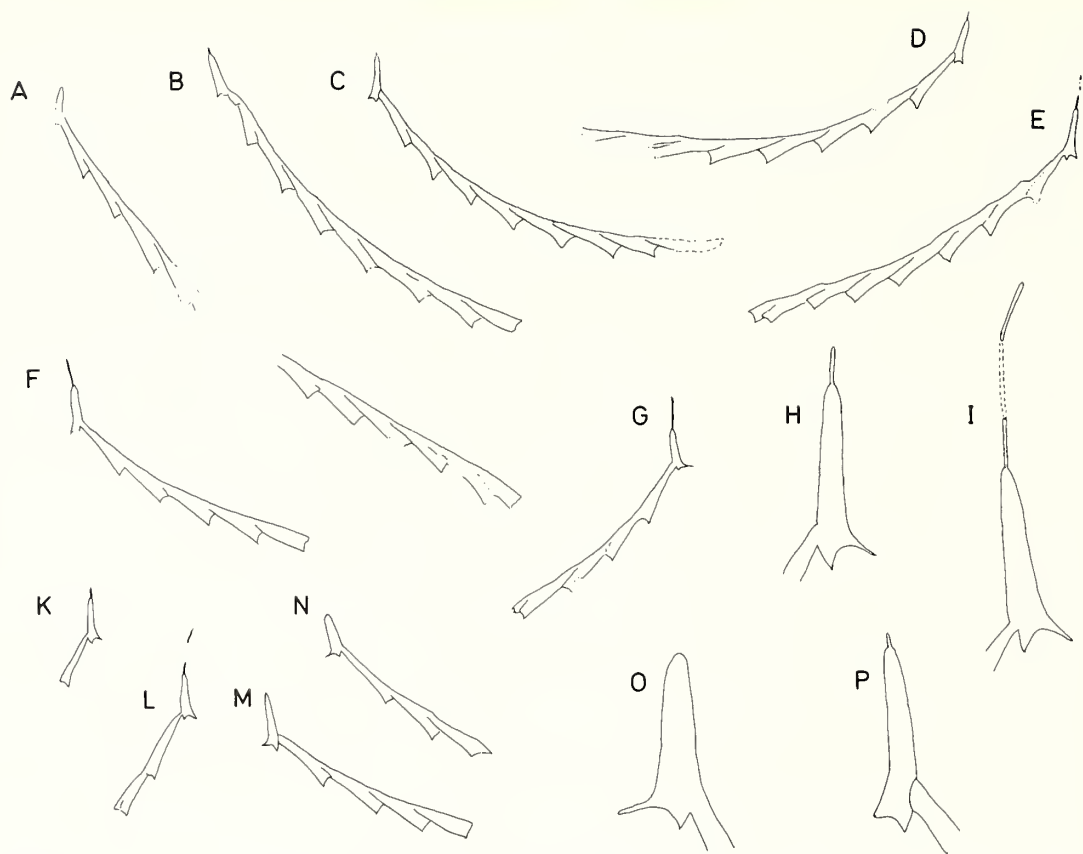
Diagnosis. *Azygograptus* with very short basal free length to sicula (< 0.2 mm); no rutellum, and no adpressed growth of th 1¹ and sicula.

Type material. The specimen figured by Moberg (1892, pl. 8, fig. 1) was selected as the lectotype by Bouček (1973). However Bouček (1973, p. 107) stated that the type specimens were in the collection of the Geological Institute of Lund, whilst they are in fact held in the type collection of the Sveriges Geologiska Undersökning. There is therefore some doubt that Bouček examined the type specimens, and unfortunately the lectotype he selected is poorly preserved.

Type locality. Flagabro-Killeröd, Scania from just below Komstad Limestone. A translation of the original description of the locality was given by Lindholm (1985, pp. 39–41). The species occurs in the uppermost part of the Toyen Shale together with *Isograptus gibberulus* (sensu Moberg, 1892), *Maeandrograptus schmalensei*, *Didymograptus mobergi*, *Expansograptus hirundo*, *E. cf. abditus*, *Pseudotrigonograptus ensiformis*, *Kinnegraptus kinnekullensis* (sensu Williams and Stevens 1988, non Skoglund 1961). The overlying Komstad limestone belongs to the *Megistaspis* (*Megistaspis*) *simon* trilobite zone (Nielsen 1985). The graptolites indicate the *I. v. lunatus* or *I. v. victoriae* biozone of the Australian zonation and the Scandinavian *D. hirundo* biozone.

Other occurrences. Though the species has been listed from a number of localities in Scandinavia the majority are probably *A. ellesi*. Only one occurrence outside the type locality has been reliably identified. This is at Graptolittaldalen, Slemmestad, Oslo Region (PMO 118:570), and is a single slab with specimens in the silvery carbonaceous preservation typical of the area. Indirect evidence which supports the occurrence is that *Isograptus gibberulus* sensu Moberg is also present at Slemmestad (Spjeldnaes 1953, pl. 1, fig. 5) and is also only known from the Moberg locality in Scania.

Description. Sicula 1.1–1.3 mm long and curves away from the stipe at the aperture which is 0.25–0.3 mm wide.



TEXT-FIG. 18 A-E, *P. Azylograptus suecicus* Moberg, from Killeröd, Scania; A, SGU 5247, lectotype, $\times 5$; B, SGU 5248, paratype, $\times 5$; C, SGU 7895, drawing in latex, $\times 5$; D, SGU 7896, proximal part in relief, distal part preserved as mould, $\times 5$; E, SGU 5247, same slab as holotype, preserved as mould, $\times 5$; P, SGU 7895, detail of sicula, $\times 20$. F-M, *A. eivionicus* Elles, from Toyen Section, Oslo, 19.43-19.55 m interval; F, PMO 118.608, $\times 5$; G, PMO 118.603-2, $\times 5$; H, PMO 118.604, $\times 5$; I, PMO 118.603-1, detail of sicula, $\times 20$; K, PMO 118.604, detail of sicula $\times 20$; L, PMO 118.603-1, $\times 5$; M, PMO 118.605, $\times 5$. N-O, *A. eivionicus* Elles, from Toyen Section, Oslo, 19.19-19.29 m interval; N, PMO 118.602, $\times 5$; O, PMO 118.602, $\times 20$.

Sicular aperture is symmetrical without rutellum. Stipe originates low on the sicula and diverges abruptly at an angle of $140-150^\circ$, leaving a basal free length to the sicula of $0.1-0.2$ mm. Stipe moderately flexed with up to 35° rotation by th 5. Thecae are slender, with stipe width at aperture of first theca $0.45-0.5$ mm; distal stipe width $0.7-0.8$ mm. Thecal separation $1.4-1.7$ mm (6-7 th/10 mm), but the first theca appears somewhat longer. Thecal inclination $14-18^\circ$.

Discussion. *A. suecicus* is easily distinguished from other members of the genus by the simple form of the sicular aperture (see Text-fig. 14) associated with the lack of adpressed growth of th 1¹ and the sicula.

Azylograptus validus Törnquist, 1904

Plate 1, fig. 13; Text-fig. 19A-L

1904 *Azylograptus validus* Moberg MS.; Törnquist, p. 27, pl. 4, figs 12-14.

Diagnosis. *Azygograptus* with higher thecal inclination (approximately 25°) than other species. Obvious adpressed growth of sicula and th 1¹ with origin of th 1¹ very high on the sicula.

Type material. LO 1755T, LO 1756t; additional topotype SGU 7555–7557, 7889–7892.

Type locality. Diabasbrottet, Hunneberg Mountain (previously called Mossebo) (see Lindholm and Maletz 1989). Moderately abundant specimens, predominantly occurring as silvery organic films on black shale. Topotype specimens came from the interval 4.74–4.89 m of the section in Erdmann *et al.* (1987, p. 112). Associated with *T. phyllograptoides*.

Other occurrences.

1. Krappertup boring in Scania (Lindholm 1981); 6 specimens at the 96.45 m level, together with *D. undulatus* in the *T. phyllograptoides* biozone.

2. Robinson Mountain, Lake District (locality A1 of Text-fig. 3); solitary, very poorly preserved specimen in medium grey mudstone (BGS Rx 1273–Rx 1274); associated with *Acrograptus filiformis*.

3. Toyen Shale, Toyen Underground Station, City of Oslo, Norway; single, poorly preserved specimen (PMO 118-571) from the interval 7.65–7.85 m (Text-fig. 2), associated with *T. phyllograptoides*.

Description. Sicula long and slender; 2.0–2.3 mm long; 0.3–0.4 mm wide at aperture. A short nema is sometimes present. Th 1¹ originates very high on the sicula, possibly from the prosicula, though this is irresolvable from available material. The stipe turns away at about 120–150° leaving 0.3–0.4 mm basal free length to sicula. Thecae slender, slowly expanding; overlap about one-half. Thecal inclination 24–26°. Stipe characters uniform with largest specimen reaching th 14.; thecal density 11–12 th/10 mm; stipe width 0.5–0.8 mm. Significant stipe curvature, stipe becoming reclined in some larger specimens.

Discussion. Törnquist (1904), in describing a few small specimens from Mossebo, remarked on the strong resemblance to *Azygograptus coelebs*. *A. validus* differs from the published descriptions of *A. coelebs* (see below) in possessing a much longer sicula and shorter thecae. Thecal inclination serves to distinguish it from other species.

Azygograptus ellesi Monsen, 1937

Plate 1, figs 1 and 11; Text-fig. 20A–S

1898 *Azygograptus suecicus* Moberg; Elles p. 514, fig. 29.

1902 *Azygograptus suecicus* Moberg; Elles and Wood p. 95, text-fig. 56; pl. 3, fig. 3a–b.

1937 *Azygograptus ellesi* Monsen, p. 205, pl. 5, figs 21, 28, ?30.

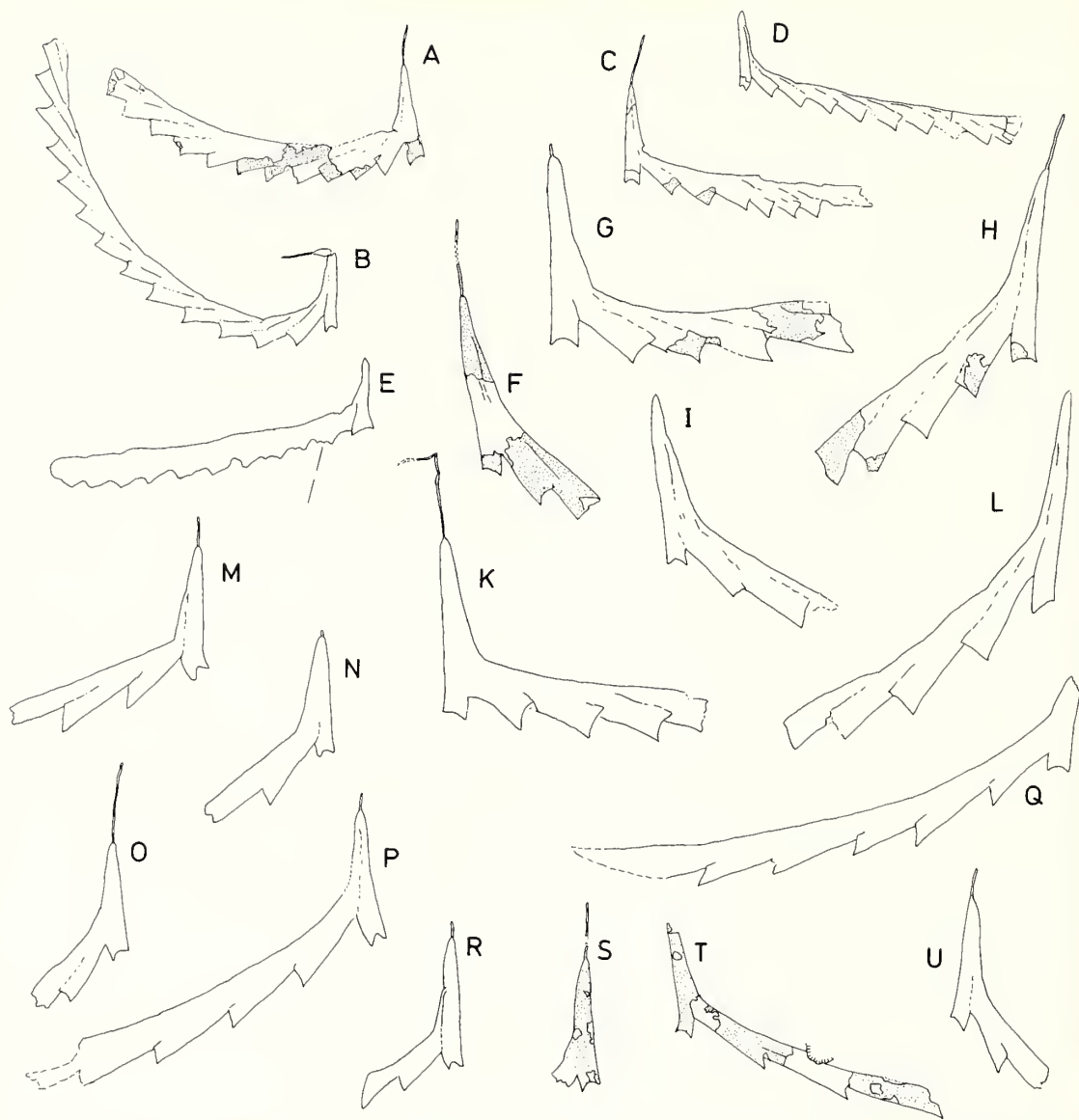
1937 *Azygograptus* cf. *suecicus* Moberg; Monsen, p. 204, pl. 5, figs 2 and 20.

1973 *Azygograptus suecicus* Moberg; Bouček, p. 107, pl. 19, figs 1–4; text-fig. 33a–g.

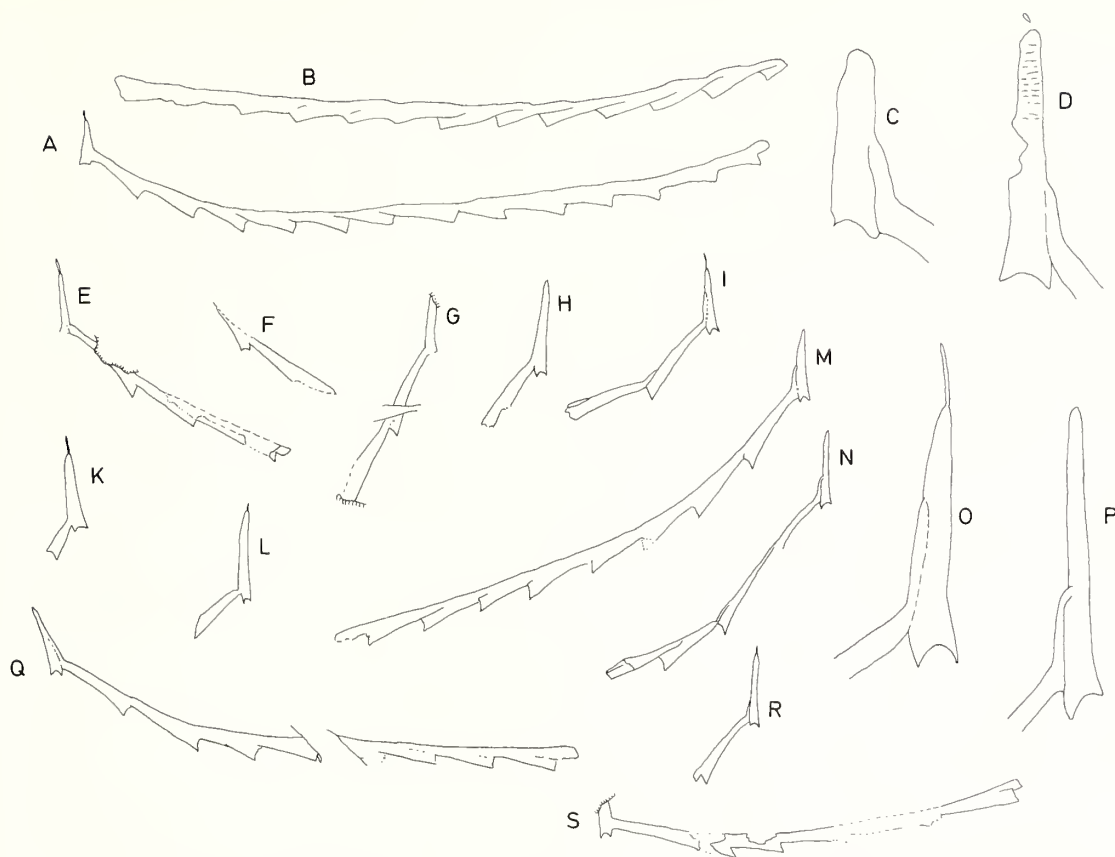
Emended diagnosis. *Azygograptus* with long sicula (1.8–2.4 mm); origin of th 1¹ in distal half of sicula and adpressed growth of th 1¹ and sicula till close to sicular aperture. Little overlap in proximal thecae.

Type material. PMO K 0288. Slab contains two specimens figured by Monsen (1937, pl. 5, figs 21 and 28) both of which were described as a ‘holotype’ in the plate explanation. The specimen represented in plate 5 figure 21 is indicated as the holotype on the label for the slab and is here adopted as the holotype; the other specimen is certainly conspecific and is regarded as a paratype. The specimen figured on plate 5, figure 30 is a distal fragment on a slab from the *P. angustifolius elongatus* biozone at Ensjo, Oslo region. Though there are several specimens of *A. ellesi* on the slab, the figured specimen is only a distal fragment and thecal spacing and inclination suggest it may not belong to *A. ellesi*.

Type locality. Toyen shale at Slemmestad, Oslo Region. The specimens come from the *P. angustifolius elongatus* biozone and are associated with *Phyllograptus* s.s., *Didymograptus* ?*protoindentus*, *Expansograptus* sp. and *Tetragraptus* cf. *serra*.



TEXT-FIG. 19. A-D, F-H, *Azygograptus validus* Törnquist from Diabasbrottet, Hunneberg Mountain, Västergötland, Sweden; A, SGU 7890B, 4.83 m level, $\times 5$; B, SGU 7556, 4.89 m level, $\times 5$; C, SGU 7557-2, 4.74 m level, $\times 5$; D, SGU 7557-1, drawing of mould, 4.74 m level, $\times 5$; E, SGU 7892, 4.79 m level, $\times 10$; G, SGU 7889B-2, 4.79 m level, $\times 10$; H, SGU 7889B-1, 4.79 m level, $\times 10$. I, *?A. validus*, BGS 1273, Robinson Mountain, Lake District, England, $\times 5$. J, K, *A. validus* from Mossebo (now Diabasbrottet), Hunneberg Mountain, Västergötland, Sweden; I, paratype, LO 1756t, $\times 10$; K, holotype, LO 1755T, $\times 10$. L, *A. validus*, PMO 118.571, 7.65-7.85 m level, Tøyen Section, Oslo, Norway, $\times 10$. M-U, *A. minutus* sp. nov. from Diabasbrottet, Hunneberg Mountain, Västergötland, Sweden, $\times 10$. M, SGU 7564, paratype, 7.09 m level; N, SGU 7593, paratype, 7.09 m level; O, SGU 7565, paratype, 7.09 m level; P, SGU 7560, holotype, 7.09 m level; Q, SGU 7562, paratype, 7.09 m level; R, SGU 7559, paratype, 7.09 m level; S, SGU 7893, paratype, 7.09 m level; T, SGU 7894, 8.29 m level; U, SGU 7561, paratype, 7.09 m level; Remarks: Diabasbrottet section as figured in Erdtmann *et al.* (1987).



TEXT-FIG. 20. *Azzyograptus ellesi* Monsen. A–D, Barf, Lake District, England; A, BM H948, $\times 5$; B, BM P7216, $\times 5$; C–D, BM P2010, two specimens on same slab, $\times 20$. E–G, Slemmestad, Norway; E, PMO K 0187, paratype, $\times 5$; F, PMO K 0288, paratype $\times 5$; G, PMO K 0288 holotype, $\times 5$. H, M–N, P–R, from 16.25–16.42 m level in Tøyen Section, Oslo, Norway; H, PMO 118.578, $\times 5$; M, PMO 118.575, $\times 5$; N, PMO 118.576, $\times 5$; P, PMO 118.576, $\times 20$; Q, PMO 118.579, $\times 5$; R, PMO 118.959, $\times 5$. I, O, SGU 7554, drawing of mould, Nipan, Jemtland; I, $\times 5$; O, $\times 20$. K, PMO K 0658, figured as *A. cf. suecicus* by Monsen (1937, pl. 5, fig. 20), Stensbergstraøe, Oslo, Norway, $\times 5$. L, S, Ensjo, Norway, from slab with stipe fragment of *A. ellesi* figured by Monsen (1937, pl. 5, fig. 30), PMO K 0657, $\times 5$.

Other occurrences.

1. Tøyen Underground Station, City of Oslo, Norway; several specimens from the section described by Erdtmann (1965). The specimens from the intervals 15.35–15.95 m and 16.25–16.42 m, within the upper part of the *P. a. elongatus* biozone, and are associated with *Pseudophyllograptus augustifolius*, *Tetragraptus bigsbyi askerensis*, *Expansograptus grandis* and *Acrograptus* sp.

2. Nipan, Jemtland; single relief specimen (SGU 7554) on a loose slab with no associated fauna; a nearby outcrop has yielded a fauna indicating the *P. densus* biozone, or higher parts of the Tøyen Shale.

3. Barf, English Lake District (NY 217267) (locality A6 of Text-fig. 3); fairly numerous specimens preserved in partial relief as limonitic internal moulds in monospecific assemblages or associated with *Pseudophyllograptus*, but the locality has yielded a very diverse fauna indicative of the *D. nitidus* biozone. BM P7216, P2010, G948.

Description. Sicula straight and slender, 1.8–2.4 mm long; 0.25 mm wide in relief specimens, a little wider (0.3 mm) in flattened specimens and with both dorsal and ventral processes on the aperture. Th 1^1 originates

at 0.6–0.75 of the sicula length and grows down along sicula until 0.1–0.2 mm above the sicula aperture. Declined stipe very slender, generally straight but may be slightly curved in some specimens. Stipe width 0.45–0.7 mm and is nearly constant throughout rhabdosome, with the only increase over the first couple of thecae. Thecal overlap one-quarter; thecal inclination 6–10°. Sicula aperture to aperture th 1: 1.9–2.2 mm, distal thecal separation: 1.7–1.5 mm (6.5–8.5 th/10 mm).

Discussion. The only measurements that can be made on the holotype are the length of th 1 (2.2 mm) and stipe width at the aperture of th 1 (0.45 mm). Both are consistent with the description given above.

Until now the majority of azygograptids from Scandinavia have been identified as *A. suecicus*, but the origin of th 1 apparent from the relief material shows this to be incorrect. The specimens described as *A. cf. suecicus* by Monsen (1937) also clearly belong to *A. ellesi* and one specimen is refigured here (Text-fig. 20κ).

The proximal development (see Text-fig. 20c,d) and stipe width (0.45–0.8 mm) of the specimens from Barf, English Lake District, are comparable to *A. ellesi*, but the sicula is somewhat shorter (1.2–1.5 mm). Thecal density is also slightly higher in the distal part of the stipe (7–9 th/10 mm) of the British specimens, which appears to result from the slightly greater thecal overlap. The specimens figured as *A. suecicus* by Elles and Wood (1902, pl. 13, fig. 3a–b) are also from Barf, for which they note the adpressed growth of th 1¹ and the sicula.

The specimens described as *A. suecicus* by Bouček (1973) from the *Tetragraptus reclinatus abbreviatus* zone of Bohemia, possess a relatively long sicula and are described as having downward growth of the initial part of th 1. The proximal development cannot be discerned on the photos, but the specimens are tentatively included in *A. ellesi*.

Azygograptus minutus sp. nov.

Plate 1, fig. 12; Text-fig. 19M–U

Origin of name. In recognition of the small size of the species.

Diagnosis. *Azygograptus* with origin of th 1¹ high on sicula and adpressed growth until close to sicula aperture associated with low thecal inclination and high thecal density (9–10 th/mm).

Type material. Holotype: SGU 7560. Paratypes: SGU 7558–7559; 7561–7565.

Type locality. Västergötland, north-eastern edge of Hunneberg Mountain, Diabasbrottet. A few specimens in association with *Paradelograptus kinnegraptoides*, *Expansograptus vacillans* and *E. holmi* on a single bedding plane in the *Didymograptus balticus* biozone, at 7.09 m in the section of Erdtmann *et al.* (1987, p. 112).

Other occurrences. None known.

Description. Slender and small species with longest specimen only 6 mm long which reaches th 7. All specimens may therefore be immature. Sicula 1.6–1.9 mm long with apertural width 0.25–0.3 mm. Th 1 originates high on the sicula and grows down adpressed for the majority of the sicula length before flexing away at an angle of 120–150°. The basal free length to the sicula is 0.2–0.4 mm and the sicula aperture has symmetrical, small, dorsal and ventral lips. Thecae slender and long, thecal inclination 10–15° and thecal overlap about a half. Thecal density 9–10 th/10 mm. Stipe is slightly flexed and reaches a maximum width of 0.6 mm; no variation along stipe has been recognized.

Discussion. *A. minutus* is characterized by its high thecal density. The only species with which it is likely to be confused is *A. validus* which also has a high origin of th 1¹. The main differences are the lower inclination of thecae in *A. minutus* and shorter sicula.

Other species which have been placed in *Azygograptus* are as follows:

1. *A. canadensis* Ruedeman, 1947, p. 357, pl. 58, figs 9–11. Glenogle Shale, Glenogle, Canada. Belongs to *Pseudazygograptus*.
2. *A. coelebs* Lapworth, 1880, p. 159, pl. 5 fig. 16a–c. This species has only been described from the Skiddaw Slate Group of the Cross Fell Inlier, Northern England, though it has been identified from Algeria (Whitman 1971). The original description was based on material from Ellergil, and the species has been recorded from Milburn Beck (Shotton 1935). The associated fauna, which includes biserial and pendent graptolites, indicates a Llanvirn age. The validity of the species is in doubt because only the two specimens (SM A18016 and BM 1027) figured by Elles and Wood (1902, pl. 13 fig. 4a–b) appear to exist and neither is adequate to characterize the species or confirm the generic placement.
3. *A. flexilis* Chen and Xia, in Mu *et al.* 1979, pp. 110–111, pl. 38, figs 13 and 14. Described from the *A. suecicus* biozone of Southwest China. The description states that th 1 grows down beside the sicula and on this feature it may be grouped with *A. ellesi*. It differs from *A. ellesi* in having a shorter sicula (1.3 vs 1.8–2.4 mm). No description is given here because the original material has not been examined. The only reason this may not be a valid species is synonymy with another Chinese species.
4. *A. fluitans* Geh, in Mu *et al.* 1979, p. 112, pl. 39, figs 1–5. Described from the *A. suecicus* biozone of Southwest China. No material of this species has been examined but it may be synonymous with *A. undulatus* (Chen Xu, pers. comm.).
5. *A. groenwalli* Monsen, 1937, p. 206, pl. 5, fig. 29. From the *Pseudophyllograptus densus* biozone, Ensjo, Oslo Region, Norway. Only known from the type specimen which is almost certainly a broken specimen of the co-occurring *Didymograptus* cf. *minutus*. The species is therefore considered a junior synonym of *D. cf. minutus*.
6. *A. hexianensis* Jiao, 1984, p. 623, text-fig. 2; pl. 2, figs 31 and 32. *A. suecicus* biozone of Hexian, Anhui. This species is difficult to interpret from illustrations but appears to belong to group 1. Occurs with *A. undulatus*, *A. suecicus* and *A. lapworthi*.
7. *A. novozealandicus* Skwarko, 1962, p. 224, text-fig. 4; fig. 6. South side of Peel Range, northwest Nelson, New Zealand, Lower Gisbornian. From the drawing alone this may be a fragment of a dichograptid, though the description states every specimen has a long nema implying a proximal end is present. However, positive identification with *Azygograptus* is not possible.
8. *A. (?) oelandicus* Bulman, 1936, pp. 46–48, pl. 2, figs 16–29; text-fig. 17. An indeterminable fragment; sicula unknown. The species was transferred to the Dendroidea as *Parvitubus oelandicus* by Skevington (1963, pp. 47–51, figs 62–72).
9. *A. prolixus* Keble and Benson, 1929, fig. 14. Northwest Nelson, New Zealand, Lower Aorere Series, Douglas zone, Cobb subzone, ?upper Arenig–Llanvirn.
10. *A. saltaensis* Loss, 1949. From the drawing this may be a fragment of an expansograptid, but the original material would need to be examined to confirm this.
11. *A. (?) simplex* Ruedemann, 1908, pp. 258–260, text-figs 163–171; pl. 14, fig. 10. A very curious form with a huge sicula and only one associated theca. Certainly not closely related to *Azygograptus*.
12. *A. undulatus* Chen and Xia, in Wang 1974, p. 157, pl. 68, fig. 4. This species has only been recognized from the *A. suecicus* biozone in Southwest China. It displays adpressed growth of th 1 and has a high origin on sicula suggesting comparison with *A. validus* or *A. minutus*. Probably a valid species. The sicular length is less than in *A. validus* or *A. minutus*, but the taxonomic importance of pro-thecal folds is uncertain. *A. fluitans* and *A. undulatus spinosus* may be junior synonyms of *A. undulatus* (Chen Xu, pers. comm.). This species has also been described from northern Spain (Gutierrez Marco and Rodriguez 1987).
13. *A. undulatus spinosus* Chen, in Mu *et al.* 1979, p. 112, pl. 38, figs 24 and 25. Described from the *A. suecicus* biozone of Southwest China. Probably synonymous with *A. undulatus* (Chen Xu, pers. comm.).
14. *A. (?) walcotti* Gurley, 1896, pp. 69, 92. Lower *Dicellograptus* biozone, Stockport, New York, USA. The species has never been redescribed but was figured by Ruedeman (1947, pl. 58, fig. 8). Its relationships remain unclear, but it might belong to *Pseudazygograptus*.

Genus JISHOUGRAPTUS Geh, 1988

Type species. *Jishougraptus mui* Geh, 1988.

Emended diagnosis. Single deflexed, uniserial stipe, dorsal margin undulate but without folds, thecae long and thin, tending to leptograptid type but not forming bundles. Thecae simple to elaborate.

Discussion. The only change made from the original diagnosis is the inclusion of simple thecae as well as elaborate. Neither of the species described below show the ventral geniculation or elaborate thecal aperture of the type species. The only difference from *Azygograptus* is the elongate, thin form of the thecae with greater overlap.

Jishougraptus novus sp. nov.

Plate 1, figs 6, 9, 10; Text-fig. 21A–N

Origin of name. Novus = new, in reference to the fact that this is the first species to show sigmoidally curved thecae.

Diagnosis. *Jishougraptus* with simple cylindrical thecae, and elongate sicula (1.8–2.4 mm).

Type material. Holotype: PMO 118-585, preserved as a mould in dark shale. Paratypes: PMO 118-580–584, 118-586–594.

Type locality. Tøyen Underground station, City of Oslo, Norway. Abundant specimens in the interval 16.15–16.25 m in the Tøyen section (see Text-fig. 2). The specimens are associated with *Tetragraptus bigsbyi divergens*, *Pseudophyllograptus angustifolius*, *Expansograptus extensus linearis*, *E. decens*, *F. grandis* and *Acrograptus* sp. Most specimens are preserved in relief, with only a few preserved as flattened films.

Other occurrences. Slemmestad, section 2b of Spjeldnaes (1985). PMO 117-553, 555. A few poor specimens collected by B.-D. Erdtmann on an excursion in 1988. The species occurs with *Oslograptus peculiaris* and *T. bigsbyi divergens*.

Description. Sicula 1.8–2.4 mm long and very slender. Short nema, up to 0.4 mm long, sometimes detectable but apex of sicula often poorly defined. Th 1¹ originates at half of sicular length and is adpressed until 0.1–0.15 mm above sicular aperture, where it diverges at 140–160°. Thecae are simple, slender and cylindrical with slight sigmoidal curvature. Prothecal folds not developed but distinct ‘ridges’ present at origins of thecae in relief specimens. Thecal separation 1.5–2.3 mm (4.5–6.5 th/10 mm) and relatively constant along rhabdosome. Stipe width at th 1 0.35–0.5 mm; distally 0.7–0.8 mm.

Discussion. *J. novus* is very similar to *J. lindholmae* and distal stipe fragments of the two species are virtually indistinguishable. However proximal development does show significant differences: *J. novus* has a sicula almost twice as long on average and much shorter th 1¹.

Jishougraptus lindholmae sp. nov.

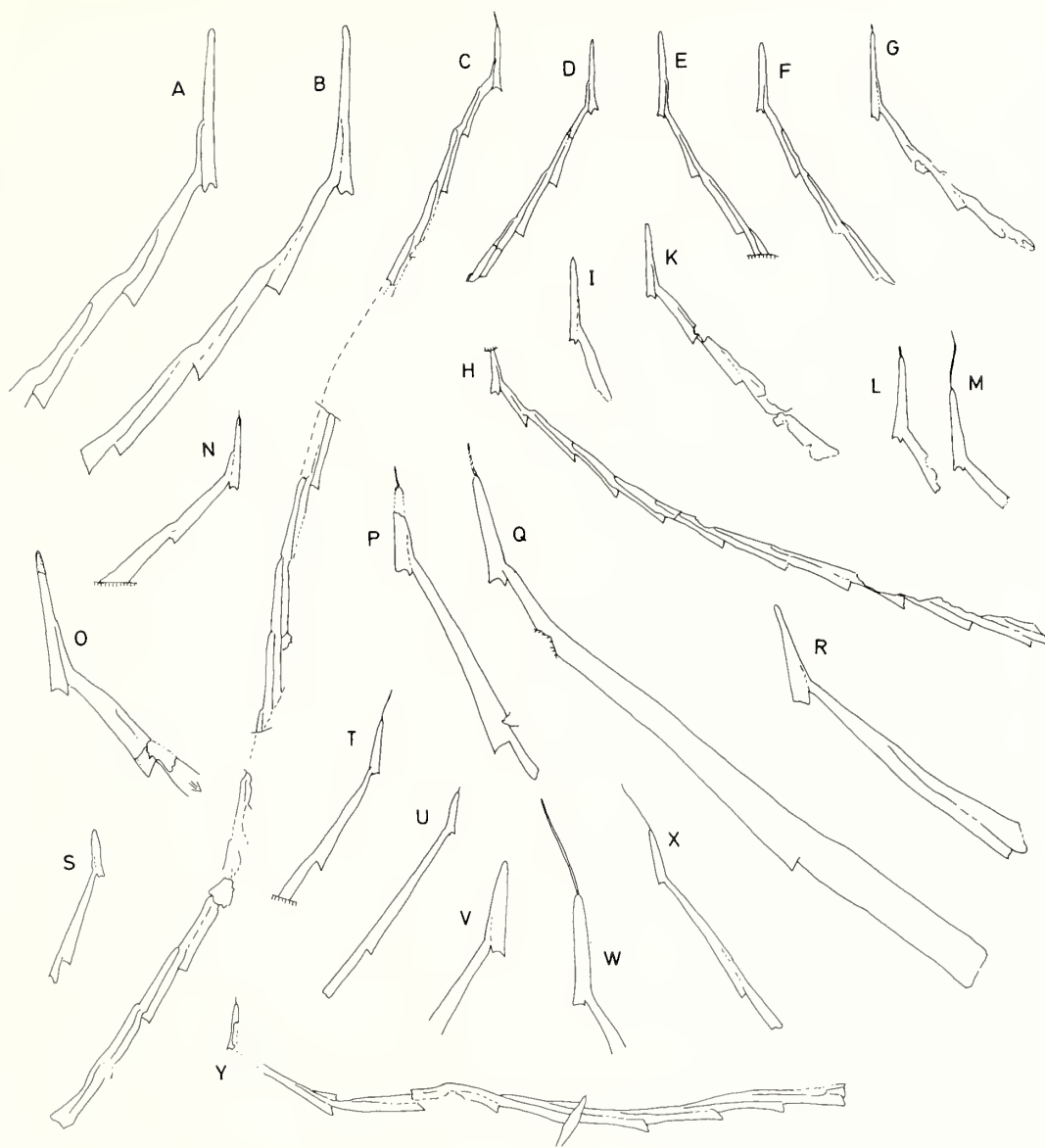
Text-fig. 21P–Y

1981 *Azygograptus* n. sp., Lindholm, p. 15, fig. 6a–b.

Origin of name. Named after Miss Kristina Lindholm (Lund University) who first recognized and described the species, though she did not name it.

Diagnosis. *Jishougraptus* with small sicula (1.0–1.5 mm) and simple, cylindrical thecae.

Type material. Holotype: PMO 118-595; flattened specimen in dark shale. Slab is crowded with other



TEXT-FIG. 21. *Jishougraptus novus* sp. nov. and *J. lindholmae* sp. nov. from the Tøyen Section, Oslo, Norway. A–O, *J. novus*, C is the holotype, the rest are paratypes, from 16.15–16.25 m interval, Tøyen Section; A, PMO 118.582–2, $\times 10$; B, PMO 118.588, $\times 10$; C, PMO 118.585, $\times 5$; D, PMO 118.592–1, $\times 5$; E, PMO 118.590, $\times 5$; F, PMO 118.589, $\times 5$; G, PMO 118.593–2, $\times 5$; H, PMO 118.582–1, $\times 5$; I, PMO 118.581, $\times 5$; K, PMO 118.592–2, $\times 5$; L, PMO 118.583, $\times 5$; M, PMO 118.583, $\times 5$; N, PMO 118.580, $\times 5$; O, PMO 118.592–2, $\times 10$. P–Y, *J. lindholmae*, Q is the holotype, the rest are paratypes, from 16.81–17.10 m interval, Tøyen Section; P, PMO 118.599–3, $\times 10$; Q, PMO 118.595, $\times 10$; R, PMO 118.600, $\times 10$; S, PMO 118.597, $\times 5$; T, PMO 118.599, $\times 5$; U, PMO 118.596, $\times 5$; V, PMO 118.597, $\times 10$; W, PMO 118.600, $\times 10$; X, PMO 118.600, $\times 5$; Y, PMO 118.596, $\times 5$.

fragments of the same species. Paratypes: PMO 118-596-600; mainly flattened specimens in dark shale. A few incomplete specimens are in very low relief.

Type locality. Toyen Underground Station, City of Oslo, Norway, from the Toyen Shale (16.81-17.10 m) within the *P. angustifolius elongatus* biozone (see Text-fig. 2). Abundant fragmentary specimens on slabs of black mudstone. Usually preserved as flattened films of silvery periderm, but a few specimens are preserved in low relief. The associated fauna comprises *P. angustifolius elongatus*, *Expansograptus* sp., *Tetragraptus isograptoides*, *T. cf. serra*, *T. reclinatus*, *Pendeograptus cf. pendens*, *Janograptus* sp., *Acrograptus gracilis* and ?*Trichograptus*.

Other occurrence. Krapperup Core in Scania (Lindholm 1981), from the zone of *P. angustifolius elongatus*.

Description. Small, slender sicula: 1.0-1.5 mm long; 0.25 mm wide at aperture. Short nema occasionally present to 0.8 mm long, but sicula apex narrow and poorly differentiated from nema. Near apex of sicula distinct corrugations apparent, probably indicating prosicula. Th 1¹ originates mid-way along the sicula and grows down adpressed to it. Thecae are very long, slender and slightly sigmoidally curved. Thecal overlap about one-half proximally and increases slowly distally. Thecal spacing: more than 3 mm proximally, 1.4-1.6 mm (6-7 th/mm) distally; thecal inclination: 5-8°. The stipe width increases slowly from 0.3-0.4 mm proximally to 0.6-0.8 mm at about th 7.

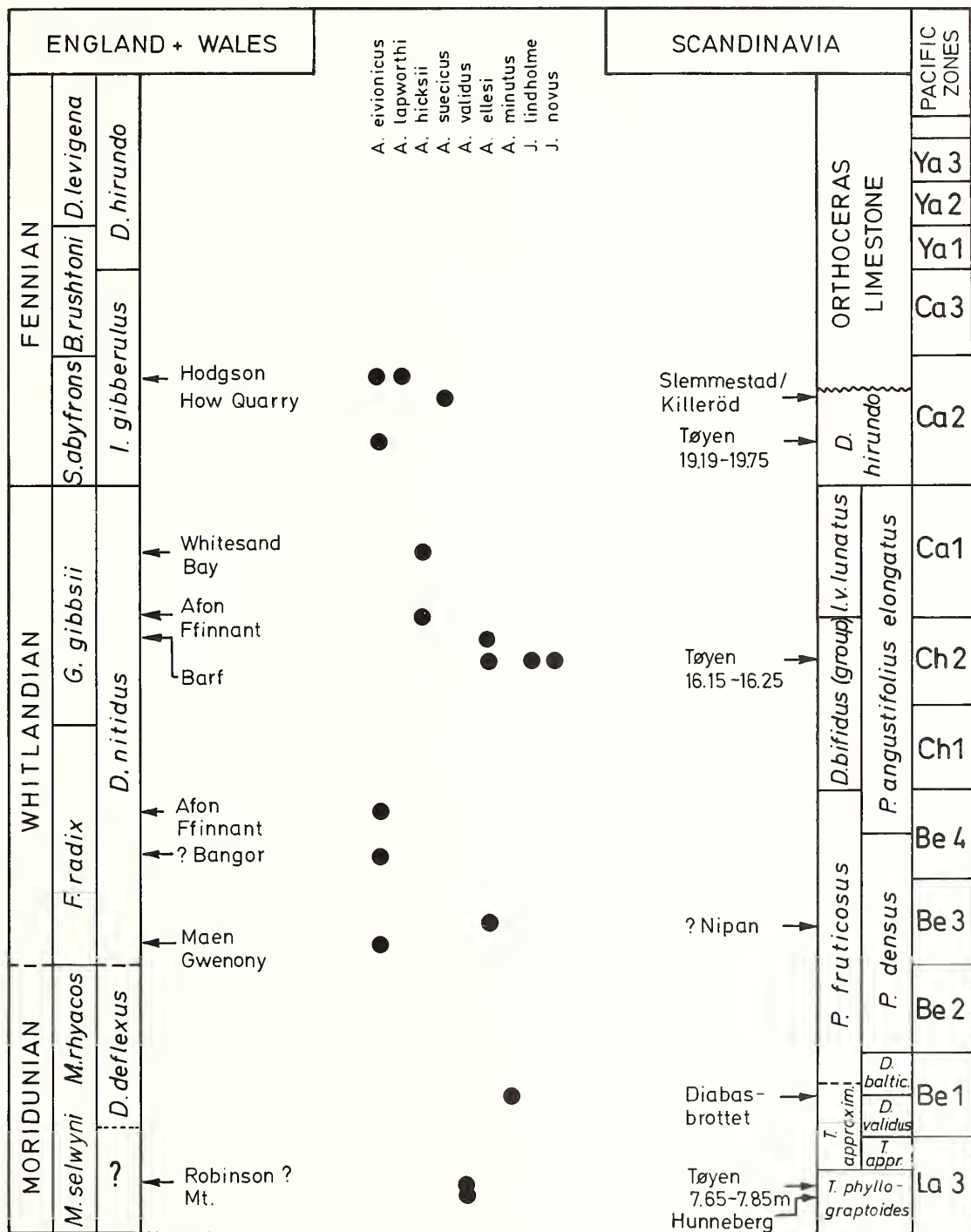
Discussion. Stipe characters distinguish *J. lindholmae* and *J. novus* from other species but do not allow distinction between them. This is only possible on features of proximal development; *J. lindholmae* has a sicula only half as long on average, and longer th 1 than *J. novus*.

The material from the Krapperup core in Scania (Lindholm 1981) is closely comparable to that described above but the description of the former would suggest some slight differences. Constrictions at the level of the aperture of the preceeding theca and the development of true prothecal folds are not seen in the Toyen specimens but such features could be the product of preservation. The prothecal folds in figure 6b of Lindholm (1981) are weakly developed and are thought to be induced by the origin of the next theca: at the point of origin of a theca a small ridge is usually visible and might be over-interpreted as a prothecal fold. In flattened material there is no evidence of prothecal folds (Lindholm 1981, fig. 6b). Constrictions of the thecal apertures could be the product of differential compaction of the apertures in otherwise relief material.

BIOSTRATIGRAPHIC USE

Azygograptus may be considered a good biostratigraphic indicator of the Arenig Series since species described from the Llanvirn (e.g. *A. coelebs*) cannot be confirmed as belonging to the genus, if valid species. However, its use in the biostratigraphic subdivision of the Series has proved more limited. Elles (1922) proposed a lineage from *A. lapworthi* through *A. eivionicus* to *A. suecicus*, but provided little evidence to support this conclusion. In China, a zone of the Ningkuoan has locally been referred to as the *A. suecicus* biozone. However, this appears to reflect an abundance of the genus at the given level rather than a limited range for the named species. Due to the difficulty in reliably identifying species from descriptions and illustrations alone, the following discussion concentrates on the evidence from Britain and Scandinavia. Unless otherwise stated, the biozone refers to the local stratigraphy from which the specimens under discussion have come (cf. difference in British and Scandinavian *hirundo* biozone (Text-fig. 22)).

The major problem in using *Azygograptus* for biostratigraphy is that it displays a number of characters which are undesirable for this purpose. The absence of *Azygograptus* from the Pacific 'province' precludes its direct use for international correlation, and the nature of its distribution suggests at least the possibility of geographically isolated populations even within the Atlantic 'province'. However, it is its facies controlled distribution, which often causes the genus to be isolated from other biostratigraphic control, that makes the possibility of using the genus for correlation desirable.



TEXT-FIG. 22. Stratigraphic distribution of *Azygograptus* and *Jishougraptus* in Britain and Scandinavia with a correlation between the two areas.

Objective evidence for the succession of species in *Azygograptus* is very limited. The Diabasrottet section on the Hunneberg Mountain has *A. minutus* overlying *A. validus*, and the Toyen section has yielded three species of *Azygograptus* and two of *Jishougraptus* but these come from a very small proportion of the overall succession. The biostratigraphic use of the genus is therefore largely dependent on ranges inferred by independent correlation of isolated occurrences (see Text-fig. 22).

The oldest species identified in the Toyen section is *A. validus* and here, as elsewhere in Scandinavia, it is only known from the *T. phyllograptoides* biozone. The overlying Scandinavian biozone, *D. balticus*, has also yielded a single species only, *A. minutus*, which is unknown outside its type locality.

Since the international correlation of the base of the Moridunian Stage (cf. Fortey and Owens 1987) is uncertain, the single specimen of *A. validus* from Robinson Mountain may be the only representative of *Azygograptus* in Britain from strata equivalent to the lowest two biozones of the Arenig in Scandinavia. The biostratigraphic use of the genus is therefore difficult to evaluate over this interval and must await evidence from a wider area.

A. ellesi appears to range through the *densus* (Nipan) and *angustifolius elongatus* (Slemmestad) biozones, and the British occurrence at Barf may reasonably be considered to come from the same time interval, though the difference in sicular length does reduce the confidence in the identification of the two populations as conspecific. The species of *Jishougraptus* that occur with *A. ellesi* at Toyen are both known only from the *P. angustifolius elongatus* biozone. The genus, based on the evidence of the type species, ranges somewhat higher.

Given the uncertainty in the correlation of the British Stages (Moridunian and Whitlandian) with the Scandinavian succession, the precise ranges of contemporary British species are unclear. *A. eivionicus* is associated with a Moridunian trilobite fauna at Arennig (Zalasiewicz 1986) and may range as high as the *gibberulus* biozone (Hodgson How Quarry). There is little to constrain independently the age of the occurrence at Bangor, but it may well be approximately contemporary with other occurrences in Wales and close to the Moridunian/Whitlandian boundary. *A. eivionicus* therefore appears to be a long ranging species of little biostratigraphic potential.

This contrasts with the species to which *A. eivionicus* may be related on the evidence of transient populations. *A. hicksii* is unknown outside South Wales and appears to be restricted to the *Gymnostomix gibbsii* biozone (late Whitlandian). *A. lapworthi* has not been found associated with any independent age control outside the type locality, where it may be placed in the *gibberulus* biozone on the basis of an isograptid associated with *D. hirundo*. Circumstantial evidence for the North Wales occurrences is compatible with a Fennian age and at present the species may be considered restricted to this interval in Britain. However, the material from Bolivia may extend the range downward. *A. suecicus* in Scandinavia is a similarly rare form and appears to be restricted to the Scandinavian *D. hirundo* biozone, and may occur contemporary with *A. lapworthi*.

In summary, neither *Azygograptus*, nor the related genus *Jishougraptus*, have species that provide useful or reliable correlative indicators between Scandinavia and Britain. Interestingly the species that do provide some hints of use are *A. ellesi* and *A. validus* which have a less restricted biofacies association. The restriction of all species of Group I, apart from *A. eivionicus*, to either Scandinavia or Britain may indicate that the Tornquist Sea was a partial barrier to migration. For this reason the British species may prove to have more potential for correlation with other peri-Gonwanan localities.

EVOLUTION OF *AZYGOGRAPTUS*

Azygograptus forms part of the adaptive radiation of the Dichograptidae that took place in the early Ordovician, and a possible origin of the genus is during the upper Tremadoc regression (cf. Erdtmann 1986; Fortey 1984). However, the evolutionary position of *Azygograptus* in this radiation is less clear, particularly with regard to whether the genus represents a mono- or polyphyletic grouping.

As illustrated in Text-figure 7, two morphological groups can be recognized in *Azygograptus* on the presence (Group 2) or absence (Group 1) of adpressed growth of th 1¹ and the sicula.

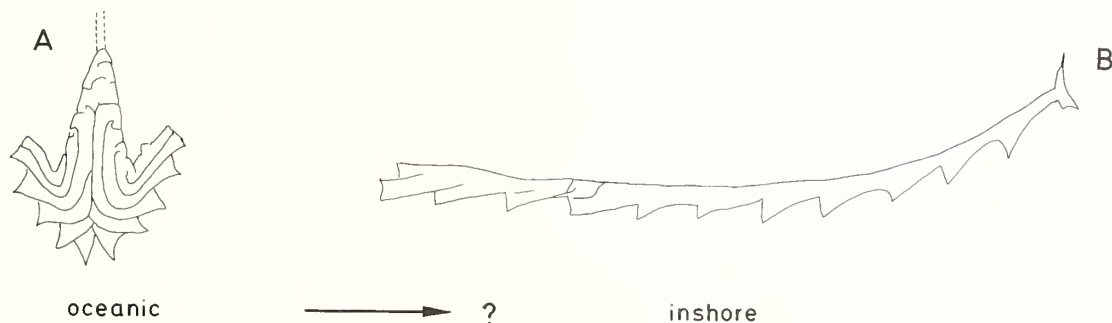
Fortey and Cooper (1986) proposed a phylogenetic classification for graptoloids on the principle that the earlier a growth decision in the development of the rhabdosome the greater its evolutionary and taxonomic significance. Within this classification *Azygograptus* was taken as separating from *Expansograptus* by suppression of dichotomy d1. However the growth decision series proposed (Fortey and Cooper 1986, table 1) has nine decisions which precede that affecting dichotomy d1, and the majority of these concern the form of the sicula and its relationship to th 1¹. The concept of growth decisions therefore implies a polyphyletic origin for *Azygograptus*, with suppression of dichotomy d1 having occurred in at least two separate lineages.

An alternative way of examining the origin of *Azygograptus* is to consider the mechanisms by which the genus may have originated and the ancestors indicated. Skevington (1966) suggested that a dimorphic population with both biramous and uniramous forms would provide a suitable ancestor for *Azygograptus*. Support for this model is provided by a population of *Kiaerograptus* (Rushton 1981) which does show variation in the number of stipes. However in this population, as in the single, questionable specimen of *Parazygograptus*, the first theca of a second stipe is present, probable th 1¹.

The presence of a vestigial stipe can be explained by failure of th 1² to be dicalycal in an ancestor with isograptid development. The origin of the second stipe in isograptid development is therefore not strictly the result of a dicalycal theca, but of the opposite direction of growth of th 1² and th 1¹. Similarly, from a dicalycal theca the new thecae grow in opposite directions. The azygograptid morphology can therefore be derived from an ancestor with either isograptid or artus development by the loss of the ability for a new theca to develop in the opposite direction to that from which it buds, and this automatically causes failure of dichotomy d1.

From the arguments presented earlier on the ecology of *Azygograptus* the more restricted ecology of the species in group 1 may indicate that they are better adapted to an *r*-selective environment. The selective pressures of such an environment are ideally suited to the formation of isolated marginal populations that may be founded on only a few individuals. Since all the species of group 1 grade into *A. eivionicus* to a greater or lesser extent, they may almost be regarded as end members in an extremely variable species, and in this respect the differences between the species are much less marked than in group 2. Therefore, despite the apparently greater number of species in group 1 the evolutionary pool represented by group 2 is probably much greater.

A possibly more important aspect of the peculiar ecology of the species in group 1 is that adaptation to an *r*-selective environment could have affected proximal development. Such an environment favours rapid development and the morphology of azygograptids can be explained as a response to this pressure in that it maximizes stipe length for a given number of budding events (see Text-fig. 23):

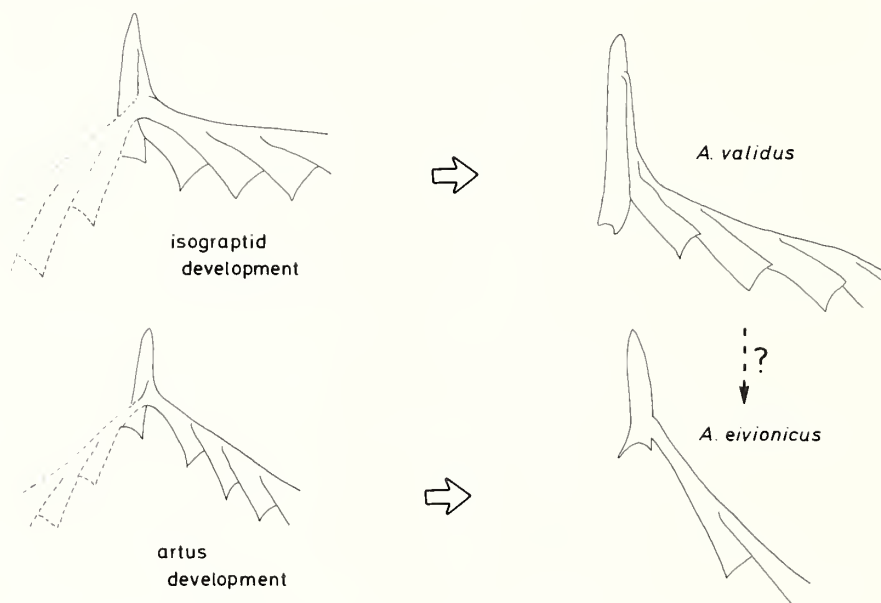


TEXT-FIG. 23. Comparison of rhabdosome form for the same number of budding events between *Pseudisograptus* (A) and *Azygograptus* (B). 11 thecae present in each.

1. abrupt metasicular origin of $th\ 1^1$ maximizes the stipe length provided by the first theca;
2. suppression of dichotomy $d1$ removes 'doubling-back' and overlap;
3. low thecal inclination with limited overlap maximizes stipe length for a given number of thecae.

An effect of the above is to maximize the separation of thecal apertures and therefore a selective pressure favouring this could be an explanation for the morphology, but the implications for proximal development remain the same.

No firm conclusion can therefore be reached on the evolutionary origins of *Azygograptus*. The oldest known species is *A. validus* and an origin from a extensiform didymograptid with isograptid development is attractive for this species (see Text-fig. 24). Once the single stipe morphology had originated the other members of the genus could have evolved from it by progressive adaptation to an *r*-selective environment. Alternatively, the species of group I, and possibly *A. ellesi*, could have evolved separately from an extensiform with artus development such as *D. simulans*, with which they appear to be geographically and ecologically associated. Therefore, the same selective pressures that may have caused convergence in rhabdosome morphology for a polyphyletic group, could also have produced differences in proximal development in a monophyletic group.



TEXT-FIG. 24. Alternative extensiform ancestors for *Azygograptus* species.

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A NEW RHYNCHOSAUR FROM THE UPPER TRIASSIC OF WEST TEXAS, AND THE BIOCHRONOLOGY OF LATE TRIASSIC RHYNCHOSAURS

by ADRIAN P. HUNT *and* SPENCER G. LUCAS

ABSTRACT. A new rhynchosaur (Reptilia, Diapsida), *Otischalkia elderae*, from the lower Dockum Group of West Texas is represented by two premaxillary fragments, two femora, and two humeri. The lower Dockum is early late Carnian (*Paleorhinus* biochron) in age. Other Late Triassic rhynchosaurs are: indeterminate hyperodapedontines from the Popo Agie Formation of Wyoming, Isalo II beds of Madagascar and an undescribed stratigraphic unit in Tanzania; *Scaphonyx* from the Wolfville Formation of Nova Scotia, Santa Maria, and Caturrita Formations of Brazil and the Ischigualasto Formation of Argentina; *Hyperodapedon* from the Maleri Formation of India and the Lossiemouth Sandstone Formation of Scotland. These occurrences of Late Triassic rhynchosaurs are of early late Carnian age. Late Triassic rhynchosaur distribution is largely controlled by the facies that are preserved at different localities. Rhynchosaurs are common in more terrestrial faunas that contain few or no phytosaurs, whereas rhynchosaurs are rare in semiaquatic faunas dominated by phytosaurs.

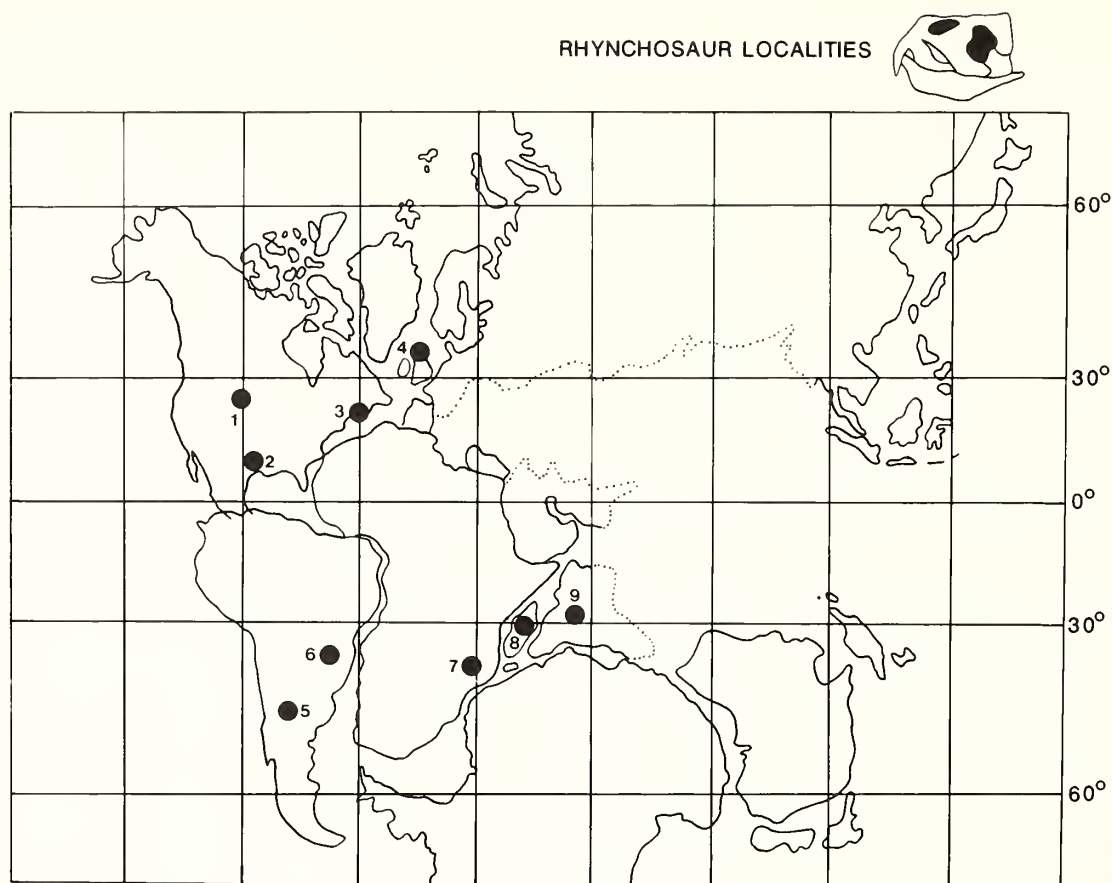
RHYNCHOSAURS are an order of primitive archosauromorph reptiles whose fossils are found in Upper Triassic strata on all continents except Antarctica and Australasia (Benton 1987; Text-fig. 1) as well as in Lower and Middle Triassic strata (Benton 1990). Several authors have mentioned the presence of rhynchosaurs in the Late Triassic of North America (Baird 1964; Elder 1978; Chatterjee 1980; Benton 1983*b*, 1987; Murry 1989; Parrish 1989*a*, 1989*b*), but none of these specimens has been adequately described.

In 1976, Sankar Chatterjee identified a fragment of a rhynchosaur premaxilla (TMM 31185-92; Pl. 1, figs 2 and 3) in the collections of the Texas Memorial Museum from the lower Dockum Group near Otis Chalk, Texas (Elder 1978; Chatterjee 1980). Subsequently, Elder (1978) identified two humeri and two femora from a nearby locality, and another premaxillary fragment from the same locality, as pertaining to a rhynchosaur. Long (in Murry 1989) recently suggested that only the premaxillary fragments pertain to a rhynchosaur and that the postcranial bones represent a large trilophosaurid.

All but one of the putative rhynchosaur specimens were collected by workers employed by the Federal Works Progress Administration from 1940–1941 from the lower Dockum Group in Howard County in West Texas (Elder 1978; Murry 1989).

The putative rhynchosaur specimens include a 65 mm-long left premaxillary fragment (TMM 31185-92) which is very similar to rhynchosaur premaxillae in having the overall shape of a flattened, tapering cylinder, in having a flat internal margin in its distal half where the two premaxillae meet (Benton 1983*a*, p. 618) and in having longitudinal striations along its distal portion (Benton 1983*a*, p. 618). Thus, we consider that TMM 31185-92 is a rhynchosaur premaxilla. TMM 31185-93 is a 17 mm-long fragment also from quarry 3A, and it represents a portion of a premaxillary indistinguishable from TMM 31185-92.

All the putative rhynchosaur postcranial remains derive from quarry 1 and include two left humeri (TMM 31025-263, Pl. 1, fig. 1, Text-fig. 2; TMM 31025-262, Pl. 1, figs 4 and 5). These



TEXT-FIG. 1. Distribution of Late Triassic rhynchosaurs: 1, Popo Agie Formation, Wyoming; 2, Dockum Group, Texas; 3, Wolfville Formation, Nova Scotia; 4, Lossiemouth Sandstone Formation, Scotland; 5, Ischigualasto Formation, Argentina; 6, Santa Maria and Caturrita Formations, Brazil; 7, unnamed unit, Tanzania; 8, Isalo II Beds, Madagascar; 9, Maleri and Tiki Formations, India.

humeri are very similar to rhynchosaur humeri (e.g. Huene 1929, pls 5, 6, 8; Huene 1942, pl. 34, fig. 4a-c; Chatterjee 1974, fig. 22a-d; Benton 1983b, fig. 49) in being very robust, with expanded ends linked by a narrow shaft with a proximal end consisting of a broad posterior plate and a narrow anteroventral deltopectoral crest, and with a distal articular surface divided into a large anterior capitellum and a large posterior trochlea. Thus, we consider that these humeri represent a rhynchosaur.

TMM 31025-266 is a reptilian femur which is very similar to rhynchosaur femora (Huene, 1938, pl. 10, 1a-f; Chatterjee 1974, fig. 25a-b; Benton 1983b, figs 33b-e and 51a-f) particularly in being robust, with moderately expanded ends, and in having a marked intertrochanteric fossa between two raised ridges on the proximal end, and in lacking a fourth trochanter. Thus, we consider that TMM 31025-266 represents a rhynchosaur. TMM 31025-264 appears to represent a deformed left femur of similar morphology.

In conclusion, it is apparent that a rhynchosaur is present in the lower Dockum Group of Howard County, Texas which is distinct from other Late Triassic rhynchosaurs and represents a

new taxon. The aims of this paper are: (1) to name and describe the new rhynchosaur from Texas; (2) to review the age relationships of all Late Triassic rhynchosaurs; and (3) to consider briefly their palaeoecology. TMM refers to the Texas Memorial Museum, Austin, Texas.

SYSTEMATIC PALAEOONTOLOGY

Class REPTILIA Laurenti, 1768

Subclass DIAPSIDA Osborn, 1903

Order RHYNCHOSAURIA (Gervais, 1859) Osborn, 1903

Family RHYNCHOSAURIDAE Huxley, 1887

Genus OTISCHALKIA gen. nov.

Derivation of name. After the abandoned settlement of Otis Chalk, Howard County, Texas (Gregory 1945, fig. 1).

Type and only species. *Otischalkia elderae* sp. nov.

Type locality. Quarry 1, site 3, near Otis Chalk, Howard County, Texas (Elder 1978, fig. 7A-B).

Horizon. Lower Dockum Group (undivided), late Carnian (late Triassic), *Paleorhinus* biochron (Hunt and Lucas 1990).

Diagnosis. As for species.

Otischalkia elderae sp. nov.

Plate 1, figs 1-7; Text-fig. 2A-C

- 1978 'Dockumensia beckerorum' Elder (unpublished), p. 66, figs 16A-B, 17A-B; 18A-C; Pl. 2, figs 1A-D and 2A-D, Pl. 3, figs 1A-D, 2A-B, 3.
- 1980 Rhynchosaur, Chatterjee, p. 58.
- 1986 Rhynchosaur, Murry, p. 120.
- 1989 Rhynchosaur, Murry, p. 108.
- 1990 Rhynchosaur, Benton, p. 84.

Derivation of name. For Ruth L. Elder who identified much of this rhynchosaur material.

Holotype. TMM 31025-263; left humerus (Pl. 1, fig. 1).

Referred specimens. TMM 31025-262, left humerus (Pl. 1, figs 4 and 5); TMM 31025-266, left femur (Pl. 1, figs 6 and 7); TMM 31025-264, left femur; TMM 31185-92, fragment of left premaxilla (Pl. 1, figs 2 and 3); TMM 31185-93, tip of premaxilla.

Diagnosis. *Otischalkia* differs from all rhynchosaurs except *Stenaulorhynchus* in having a hook on the supinator process of the humerus, and from *Stenaulorhynchus* in having a narrower proximal than distal end to the humerus, a much smaller and more discrete deltopectoral crest, and a larger capellum than trochlea on the distal humerus.

Description. The left premaxillary fragment identified by Chatterjee from quarry 3A (TMM 31185-92; Pl. 1, figs 2 and 3) was described above. TMM 31185-93 is broken at both ends, but only a few millimetres are probably missing from the tapering distal end. TMM 31185-93 also tapers proximally.

The holotype humerus of *Otischalkia*, TMM 31025-263 (Pl. 1, fig. 1; text-fig. 2A-C), and the referred humerus TMM 31025-262 (Pl. 1, figs 4 and 5), are very similar in morphology. These humeri are relatively short and robust with greatly expanded ends, with an angle of torsion between the ends of about 55°, and a narrow shaft linking them. The proximal end consists of a broad posterior plate and a relatively broad anteroventral deltopectoral crest. The shaft is narrow and elliptical in cross-section. Like *Hyperodapedon* (Benton 1983b, p.

668), the distal end has a large anterior capitellum for articulation with the radius and a posterior trochlea for the ulna. The supinator crest above the ectepicondylar groove has a hook-like projection.

The femur of *Otischalkia* (Pl. 1, figs 2 and 3) is robust, with a relatively straight shaft, a well-developed intertrochanteric fossa and no fourth trochanter. TMM 31025-266 (Pl. 1, figs 6 and 7) is a robust femur with a relatively straight shaft. Proximally, the internal trochanter forms a broad projection, separated from a large ovoid articular surface by an intertrochanteric fossa. The distal articular surface is divided into two distinct condyles, both of which may have been for the tibia (Benton 1983b).

Discussion. The *Otischalkia* humeri differ greatly from the elongate gracile humerus of *Trilophosaurus* (Gregory 1945, Pl. 27, figs 1–3; *contra* Long, in Murry 1989). Although rhynchosaur humeri are conservative in their morphology, the Texas specimens differ from the humeri of other rhynchosaurs. The Texas rhynchosaur differs from *Hyperodapedon gordonii* in having a distal expansion of the humerus that is as wide as the proximal end, and from all Late Triassic rhynchosaurs in having a hook-like process on the supinator crest. The morphology of the supinator process in *Otischalkia* is very like that of the Middle Triassic *Stenaulorhynchus* which also has a hook on the supinator process (Huene 1938, pl. 7, fig. 3a–d). However, the humerus of *Stenaulorhynchus* differs from the Texas humeri in having a greatly expanded proximal end which is wider than the distal end, a much longer and narrow shaft between the expanded ends and in having a much larger capitellum than trochlea on the distal end (Huene 1938, pl. 7, fig. 3A–D; Pl. 1, figs 4, 5; Text-fig. 2A–C).

TMM 31025-266 is more gracile than femora of *Hyperodapedon* (Chatterjee 1974, fig. 25a–b; Benton 1983a, fig. 33b–e) and apparently differs from all other rhynchosaurs in having an internal trochanter that extends almost to the proximal articular surface, although this feature may be partly due to poor preparation. TMM 31025-266 is very different in morphology from *Trilophosaurus* femora (*contra* Long in Murry 1989) in: (1) being more robust; (2) not being strongly, longitudinally sigmoidal; and (3) in having less offset distal condyles (Gregory 1945, pl. 29, figs 5 and 6).

Lacking cranial material, it is not clear what subfamily this taxon belongs to. But, as all Late Triassic rhynchosaurs apparently pertain to the Hyperodapodontinae, we tentatively assign the Texas taxon to this subfamily.

LATE TRIASSIC RHYNCHOSAUR TAXONOMY AND DISTRIBUTION

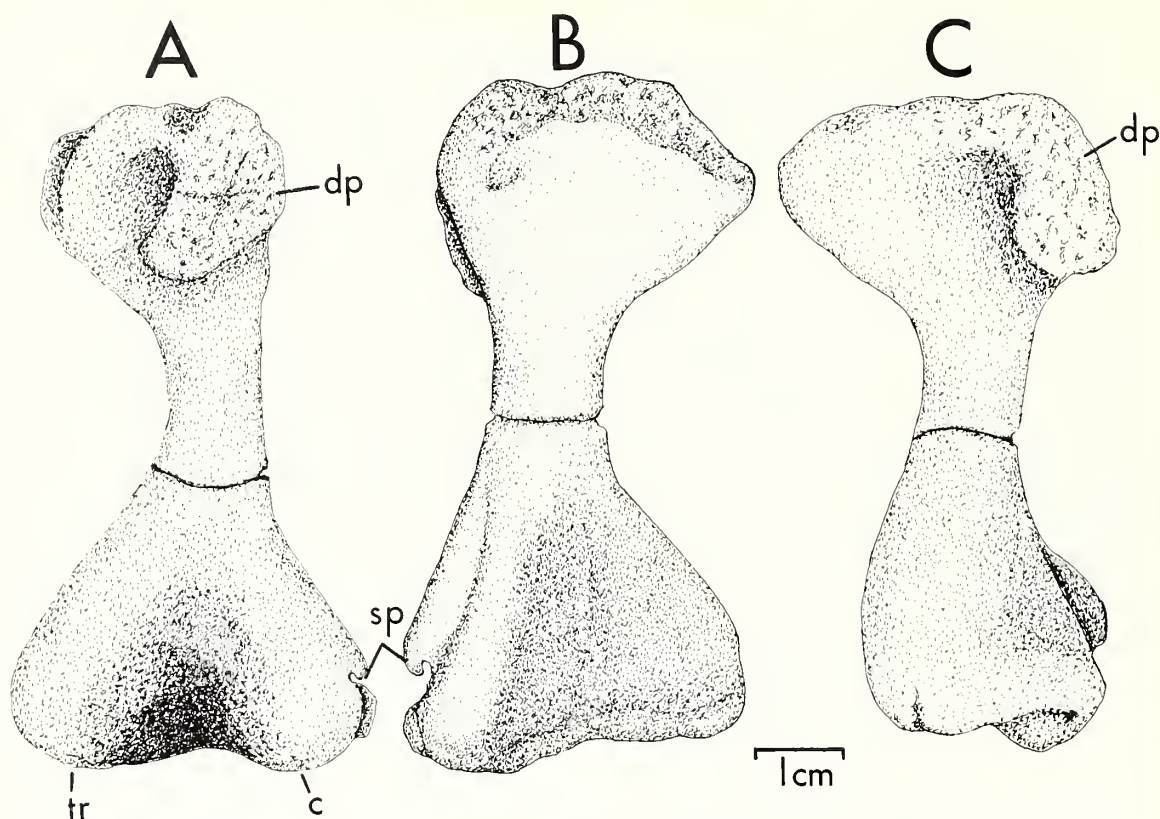
Western United States. Hotton (in Parrish 1989a, p. 362; 1989b, p. 237; Hotton oral comm., 1990) reports finding fragmentary remains of a rhynchosaur from the Popo Agie Formation, south of the Big Horn Mountains in north-central Wyoming. Parrish (1989a, p. 362; 1989b, p. 237) reported the presence of rhynchosaur bones from the *Placerias* quarry of northeastern Arizona in the lower Chinle Formation. R. A. Long (oral comm. 1990) believes that these specimens represent a large trilophosaur, but, pending publication of these specimens, we tentatively assume that they represent a rhynchosaur. Murry (1989) reported a ‘rhynchosaur’ in the Norian Redonda Formation in east-central New Mexico, but there is no evidence of any animal similar to a rhynchosaur in this assemblage (Hunt 1991).

EXPLANATION OF PLATE 1

- Fig. 1. *Otischalkia elderae* gen. et sp. nov.; holotype left humerus (TMM 31025-263); dorsal view, $\times 0.65$.
 Figs 2 and 3. *Otischalkia elderae* gen. et sp. nov.; left premaxillary fragment (TMM 31185-92). 2, lateral view.
 3, mesial view. Both $\times 1.9$.
 Figs 4 and 5. *Otischalkia elderae* gen. et sp. nov.; left humerus (TMM 31025-262). 4, dorsal view. 5, ventral view. Both $\times 0.65$.
 Figs 6 and 7. *Otischalkia elderae* gen. et sp. nov.; left femur (TMM 31025-266). 6, posterior view. 7, anterior view. Both $\times 0.65$.



HUNT and LUCAS, *Otischalkia elderae*



TEXT-FIG. 2. *Otischalkia elderae* gen. et sp. nov.; holotype left humerus (TMM 31025-263). A, posteroventral view. B, anterodorsal view. C, anteroventral view. Abbreviations: c, capitellum; d, deltopectoral crest; sp, supinator process; tr, trochlea.

Canada. Baird (1964) first mentioned rhynchosaur specimens from the Wolfville Formation of Nova Scotia, but they have never been adequately described. The presence of one longitudinal groove in the maxilla of the Wolfville specimens and the absence of lingual teeth on the maxilla (Chatterjee 1980) places them in the subfamily Hyperodapedontinae (Chatterjee 1969, 1974; Benton 1983*b*, 1987). The only member of this subfamily that lacks lingual dentition on the mandible (Chatterjee 1980), and a single tooth row on the dentary (Benton 1990), like the Wolfville taxon, is *Scaphonyx*. Thus, pending formal description, we assign the Wolfville specimens to *Scaphonyx* sp.

Brazil. Woodward (1907) named the rhynchosaur *Scaphonyx fischeri* from the Santa Maria Formation of Brazil. Huene (1926) erected several other taxa of rhynchosaurs from the Santa Maria but these have all been synonymised subsequently with *S. fischeri* (Huene 1942; Sill 1970). *Scaphonyx* is restricted to the 'Scaphonyx assemblage zone' of the upper Santa Maria Formation (Barberena *et al.* 1985). Barberena *et al.* (1985) also reported the discovery of a probable new species of *Scaphonyx* in the Caturrita Formation which overlies the Santa Maria, but the specimens have not been described.

Argentina. Sill (1970) described specimens from the Ischigualasto Formation of western Argentina as *Scaphonyx sanjuanensis*. *S. sanjuanensis* is only slightly different from the better known *S. fischeri* and may be synonymous (Benton 1987).

Scotland. All rhynchosaur specimens from the Lossiemouth Sandstone Formation of eastern Scotland are referable to the hyperodapedontine *Hyperodapedon gordonii*, which has been the subject of many articles, the last of which is an extensive monograph by Benton (1983b).

Morocco. Dutuit (1976) described *Acrodenta irerhi* from the middle of the Argana Formation in Morocco as a possible rhynchosaur, but this taxon is now considered to be captorhinid (Dutuit pers. comm. 1990).

Tanzania. Boonstra (1953) named two species of rhynchosaur, *Scaphonyx stockleyi* and *S. africanus*, from an unknown locality in the Tunduru district of what is now Tanzania. Chatterjee (1980) erected the genus *Supradapedon* for *S. stockleyi*. We agree with Benton (1983b, p. 712) that *Supradapedon* could be a large *Scaphonyx* or *Hyperodapedon*, and we refer *Supradapedon* to *Hyperodapedontinae* indeterminate. The holotype of *Scaphonyx africanus*, which is the proximal third of a weathered femur, is indeterminate, and thus this taxon is a *nomen dubium*.

Madagascar. Buffetaut (1983) named *Isalorhynchus genovefae* for a rhynchosaur maxilla from the Isalo II Beds which lacks lingual dentition. It is characteristic of the *Hyperodapedontinae* that they lack lingual teeth on the maxilla (Benton 1983b). The Madagascar genus contains only one species whose holotype is not diagnostic below the subfamily level (Benton 1987).

India. Huxley (1869) referred rhynchosaur tooth plates from the Maleri Formation to *Hyperodapedon gordonii*. Feistmantel (1880) mentioned the occurrence of rhynchosaurs in the Tiki Formation. Lydekker (1881) named these specimens *Hyperodapedon huxleyi*, and Huene (1938) erected the genus *Paradapedon* for this species. Benton (1983b) concluded that the Indian rhynchosaur should be considered a species of *Hyperodapedon*, *H. huxleyi*.

PALAEOECOLOGY OF LATE TRIASSIC RHYNCHOSAURS

Rhynchosaurs had a cosmopolitan distribution during the Late Triassic (Text-fig. 1), but their relative abundance varies considerably between faunas. Faunas rich in rhynchosaurs (Santa Maria, Ischigualasto, Lossiemouth Formations) all occur in Gondwanaland with the exception of the Lossiemouth, and contemporaneous faunas depauperate in rhynchosaurs (lower Dockum, Popo Agie, Chinle, Wolfville Formations) all occur in Laurasia. This distribution corresponds to two broad palaeobotanical provinces, characterized in the south by the *Dicroidium* flora and in the north by a 'cycadophyte'/fern/conifer flora (Tucker and Benton 1982; Benton 1983a; Olsen and Galton 1984). However, it should be noted that, except for Lossiemouth, in Laurasia, faunas rich in semiaquatic phytosaurs and metoposaurs, represent different facies than the southern Gondwanaland faunas dominated by terrestrial animals (Benton and Walker 1985). Thus, we would expect the semiaquatic and more terrestrial facies to produce different floras. Thus, although we recognise that there are two different provinces in the Late Triassic, we believe that many differences between the northern and southern faunas are ecological in nature as previously suggested (e.g. Benton 1983a; Benton and Walker 1985). In strong support of this notion, we note the recent recognition of characteristic elements of the southern faunas in Laurasia. These include the occurrence of *Scaphonyx* in the Wolfville Formation of Nova Scotia and other rhynchosaurs in Wyoming, Texas, and Scotland, the dicynodont *Ischigualastia* in the Santa Rosa Formation of New Mexico (Lucas and Hunt 1991), the ictidosaur *Pachygenelus* in the Cooper Formation of Texas (Chatterjee 1983), and a southern-Gondwana-aspect fauna in Virginia (Olsen 1989b).

BIOCHRONOLOGY OF LATE TRIASSIC RHYNCHOSAURS

Prior to the 1970s, several of the rhynchosaur-bearing formations, principally those in South America, that we now consider to be Late Triassic in age, were assigned to the Middle Triassic

(Romer 1962, 1966, 1970). However, now all the rhynchosaur-bearing formations reviewed above are considered to be late Carnian in age (e.g. Olsen and Sues 1986; Text-fig. 3) or possibly early Norian (Benton and Walker 1985). Our review of the evidence for the age of Late Triassic rhynchosaurs indicate they are all of probable late Carnian age.

Two of the rhynchosaur records discussed above are from stratigraphic units with poor age control. The hyperodapedontine from Tanzania was collected from beds of unknown age (Boonstra 1953), which have subsequently been assigned to the ?Upper Triassic because of the presence of the rhynchosaur (Chatterjee 1980). The Madagascan hyperodapedontine is from the Isalo II beds (middle Isalo Group; Buffetaut 1983) which have been considered Rhaetic (on the basis of phytosaurs and metoposaurs) to Liassic (on the basis of ammonites) in age (Besaire and Collignon 1960; Guth 1963; Westphal 1970; Dutuit 1978). However, the presence of unidentifiable phytosaurs and metoposaurs in the lower part of the unit gives no greater age precision than Late Triassic. Buffetaut (1983) suggests that the rhynchosaur from the basal beds of Isalo II is a rhynchosaurine and thus of Middle Triassic (Ladinian) age. Furthermore, the Isalo rhynchosaur is a hyperodapedontine (Benton 1987) and thus is probably of Late Triassic age, which is in agreement with other faunal evidence for the age of these beds.

Four of the remaining occurrences of Late Triassic rhynchosaurs are from faunas that contain the phytosaur *Paleorhinus* (Popo Agie, Chinle, lower Dockum and Maleri). *Paleorhinus* is important to Late Triassic biochronology because it is the only terrestrial vertebrate also known from marine strata and thus provides a means of correlating terrestrial faunas directly to marine stages (Huene 1939b; Hunt and Lucas 1991). The *Paleorhinus* specimen from marine strata is from the Opponitzer Beds near Lunz in Austria which are of Tuvanian (late Carnian) age (Janoscheck and Matura 1980; Zapfe written comm. 1989). Thus, in the absence of any conflicting data we assign all *Paleorhinus*-bearing strata to the *Paleorhinus* biochron of late, but not latest, Carnian age (Hunt and Lucas 1990). Pollen data, where available, support these age assignments (Dunay 1972; Dunay and Fisher 1979; Kumaran and Matheswari 1980; Litwin 1986). This means the rhynchosaur occurrences in the Popo Agie, lower Dockum, lower Chinle, and Maleri are of late Carnian age.

The faunas of the Ischigualasto Formation of Argentina and the upper Santa Maria Formation of Brazil share several taxa in common, including *Scaphonyx*, the aetosaur *Aetosauroides* (Casamiquela 1960; Barberena *et al.* 1985), and the dinosaur *Staurikosaurus* (Colbert 1970; Brinkman and Sues 1987). Faunal differences between these two units include the presence of

PERIOD	STAGE	SUB-STAGE	BIOCHRON	United States			Canada	Brazil	Argentina	Scotland	India
				Wyoming	Arizona	Texas					
LATE TRIASSIC	Carnian	late			CHINLE FORMATION Petrified Forest Member (lower part) Shinarump Member		WOLFVILLE FORMATION	CATURRITA FORMATION	ISCHIGUALASTO FORMATION	LOSSIEMOUTH SANDSTONE FORMATION	
			<i>Paleorhinus</i> biochron	POPO AGIE FORMATION		LOWER DOCKUM GROUP		SANTA MARIA FORMATION			MALERI FORMATION
	middle										

(H) Hyperodapedont (C) Otischalkia (S) Scaphonyx (R) undescribed/undagnostic rhynchosaur

TEXT-FIG. 3. Correlation of Upper Triassic rhynchosaur-bearing strata.

herrerasaurs and an ornithischian in the Ischigualasto and more specimens of therapsids in the Argentinian than Brazilian strata (Barberena *et al.* 1985). These differences are probably ecological in origin and thus there appears to be no basis for the widely held belief that the Santa Maria as a whole is slightly older than the Ischigualasto (e.g. Sill 1969; Benton 1988). The Caturrita Formation, which overlies the Santa Maria Formation in Brazil, shares *Proterochampsia*, *Scaphonyx*, and *Exaeretodon* with the Ischigualasto (Barberena *et al.* 1985). It appears that the Caturrita represents a more Ischigualasto-like facies than the upper Santa Maria, and that both are age equivalents of parts of the Ischigualasto Formation of Argentina (Barberena *et al.* 1985, fig. 8). These formations are usually considered ?middle-late Carnian in age (e.g. Benton 1988). There are however, problems in correlating these faunas with those of Laurasia and northern Gondwanaland because of marked ecological differences. The northern faunas, which are dominated by semi-aquatic tetrapods, have been referred to the metoposaur/phytosaur empire and the southern faunas, which are dominated by terrestrial tetrapods, to the rhynchosaur/diademodontid empire (Tucker and Benton 1982; Benton 1983a). However, we believe that there is growing evidence that the Brazilian and Argentinian faunas, containing rhynchosaurs, are of late Carnian age. Lucas and Hunt (1991) recently recognised the dicynodont *Ischigualastia* from post-*Paleorhinus* biochron strata of late Carnian age in New Mexico. This taxon is otherwise restricted to the Ischigualasto Formation. Late Carnian (post-*Paleorhinus* biochron) strata in the American Southwest also include staurikosaurid dinosaurs similar to *Staurikosaurus* from the Ischigualasto and Santa Maria Formations (Murry and Long 1989; Hunt and Lucas 1989; Hunt 1990). In addition, we recognise the rhynchosaur *Scaphonyx* in the Wolfville Formation of Nova Scotia which is also late Carnian in age (Olsen 1989a). *Scaphonyx* also occurs in the Ischigualasto, Santa Maria, and Caturrita Formations. Thus, we consider that these South American formations are of late Carnian age, based on the evidence of the distribution of *Ischigualastia*, *Scaphonyx*, and staurikosaurids.

However, to refine the age of the Ischigualasto, Santa Maria, and Caturrita Formations, we must further consider the age of the Wolfville Formation. The Wolfville fauna (Baird and Olsen 1983; Olsen 1989a) includes taxa known elsewhere from the *Paleorhinus* biochron in Texas ('*Metoposaurus*' *bakeri*) and from post-*Paleorhinus* biochron, late Carnian strata of the American Southwest (cf. *Stagonolepis*). There are no pollen (Traverse 1983) or other data to constrain further the age of the Wolfville. However, as the *Ischigualastia* occurrence in New Mexico is in undoubtedly post-*Paleorhinus* strata, we believe that it is probable that all *Scaphonyx*-bearing strata (Wolfville, Ischigualasto, Santa Maria, Caturrita) are of post-*Paleorhinus* biochron age.

The age of the Lossiemouth Sandstone Formation of Scotland has been the subject of debate (Benton and Walker 1985; Olsen and Sues 1986). At the generic level, the Lossiemouth shares *Hyperodapedon* with the Maleri Formation (Benton 1983b) of the *Paleorhinus* biochron and *Stagonolepis* with post-*Paleorhinus*, late Carnian strata of the American Southwest (Walker 1961; Murry and Long 1989). In addition, the Lossiemouth shares the procolophonid *Leptopleuron* with the Wolfville (Baird and Olsen 1983), possibly at the specific level (Olsen and Sues 1986). We thus tentatively refer the Lossiemouth to a post-*Paleorhinus* biochron (late Carnian) age based on the procolophonid correlation with the Wolfville.

In conclusion, all Late Triassic hyperodapedontine rhynchosaurs that can be dated with any accuracy are of late Carnian age (Text-fig. 3). The faunas that contain rhynchosaurs are both of *Paleorhinus*-biochron and post-*Paleorhinus*-biochron age. *Scaphonyx* is restricted to post-*Paleorhinus* biochron (Wolfville, Santa Maria, Caturrita, Ischigualasto) strata whereas *Hyperodapedon* occurs in both *Paleorhinus*-biochron (Maleri) and post-*Paleorhinus*-age strata (Lossiemouth).

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ANATOMY, PATTERNS OF OCCURRENCE, AND NATURE OF THE CONULARIID SCHOTT

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ABSTRACT. Conulariid specimens that terminate adapically in a transverse wall, or schott, have been interpreted in several ways. These interpretations have been based more on analogy with extant organisms than on evaluation of fossil material. Currently favoured interpretations are that (1) schott-bearing specimens represent individuals that were severed, in life, by currents; (2) schott-bearing specimens were free-swimming individuals; (3) schott-bearing specimens represent non-injured, sessile individuals that retracted the apical part of their soft body toward the oral end, as part of their normal life history. Examination of the test cavity of conulariid specimens that do not terminate in a schott, and analysis of the frequency of occurrence of schott-bearing specimens in low- versus high-energy sedimentary deposits, indicate that the most likely interpretation of schott-bearing specimens is that they represent living individuals severed by currents. Proponents of a scyphozoan affinity for conulariids have generally interpreted schott-bearing specimens as conulariid medusae, one of the alternatives not favoured by the present analysis. In spite of this, the interpretation of schott-bearing specimens as severed individuals is consistent with the hypothesis that conulariids and scyphozoans were closely related.

PREVIOUS discussions of the mode of life and life history of conulariids have presented compelling evidence that conulariid specimens terminating in a narrow apex (Text-fig. 1A) were sessile animals, either free-standing and attached at the apex to shell material or other substrates, or embedded in massive sponges or bryozoans (e.g. Sinclair 1948; Finks 1955, 1960; Rooke and Carew 1983; Babcock *et al.* 1987; Harland and Pickerill 1987; Van Iten 1991a). Yet disagreement persists as to the nature of conulariid specimens whose apical end, now truncated some distance above the apex, terminates in a more or less smooth, generally convex transverse wall (Text-fig. 1B). This structure, referred to by Kiderlen (1937) as the schott (the German word for bulkhead), was originally interpreted as one of a series of internal septae, homologous to the septae of nautiloid cephalopods (Hall 1847). Although schott-bearing specimens have been found that exhibit one or two additional schotts above the terminal one (Babcock and Feldmann 1986a; see also below), it is now agreed that the conulariid schott and nautiloid septa are not homologous structures (e.g. Werner 1966, 1967; Bischoff 1978; Grasshoff 1984; Babcock and Feldmann 1986a).

More recent discussions of the nature of the conulariid schott have focused on one or more of the following three alternatives: (1) the schott was a cicatrix, produced in response to severance of the body by currents (Werner 1966, 1967); (2) the schott was an autotomy scar, produced when the adult conulariid detached from its apical end and assumed a free-swimming mode of life (e.g. Kiderlen 1937; Bouček 1939; Termier and Termier 1949, 1953; Moore and Harrington 1956; Chapman 1966; Kozłowski 1968; Bischoff 1978; Grasshoff 1984); (3) the schott was a regular growth feature, produced upon attainment of a certain age (Sinclair 1948; Babcock and Feldmann 1986a). With the exceptions of Termier and Termier (1949, 1953) and Kozłowski (1968), advocates of the hypothesis that the conulariid schott was produced in response to assumption of a free-swimming mode of life interpret schott-bearing conulariids as similar to medusae of scyphozoan cnidarians, a group that has been widely regarded as the most likely candidate for an extant nearest relative of conulariids (e.g. Kiderlen 1937; Bouček 1939; Moore and Harrington 1956; Chapman 1966; Werner 1966, 1967; Bischoff 1978; Grasshoff 1984; Van Iten 1991b). Their interpretation of



TEXT-FIG. 1. A, *Archaeoconularia granulata* (Hall); AMNH 791; Middle Ordovician (Trenton Group); New York, USA; two specimens, both broken just above the apex and with their apical end (arrows) situated immediately adjacent to a straight-shelled nautiloid (probably *Endoceras proteiforme* Hall), $\times 0.88$. B, ?*Conularia* sp.; UMMP 259; Upper Devonian (English River Siltstone); southeast Iowa, USA; crumpled specimen terminating in a prominent, outwardly convex schott, $\times 1$.

the conulariid schott, here designated the alternation of generations hypothesis, is based on analogy with scyphozoans exhibiting alternating polypoid and medusoid life stages.

Werner (1966, 1967), himself a proponent of a scyphozoan affinity for conulariids, proposed that schott-bearing specimens represent polypoid individuals that were severed by currents, in life, and survived to heal their damaged apical end as they lay on their side. His interpretation, here designated the severance by currents hypothesis, is based on the observation that conulariid tests are often extremely thin (with tests 30 or more cm long but commonly less than 0.01 cm thick; Van Iten in prep.), and on analogy with coronatid scyphozoan polyps whose theca and soft parts have been severed experimentally. As documented by Werner (1966, 1967) and Chapman and Werner (1972), coronatid polyps that survive severance cover exposed soft tissues by producing a thin, smooth sheet of periderm that is similar in microstructure and gross morphology to the conulariid schott.

The third alternative, offered with essentially no support, suggests that when conulariids reached a certain age, they retracted the apical part of their soft body toward the aperture, producing a schott to seal off the portion of the test cavity just abandoned. This interpretation will be referred to here as the apical retraction hypothesis. (A similar hypothesis, proposed by Babcock and Feldman (1984, p. 17), is that conulariids were pseudoplanktonic organisms and that 'at certain points in their life cycle, sections of the periderm at the apex divided along the last-formed transverse wall [schott] and fell to the ocean floor'.)

The present paper seeks to evaluate the foregoing interpretations of the conulariid schott through analysis of its occurrence within conulariids, and through analysis of patterns of occurrence of schott-bearing specimens with respect to sedimentary facies. A critical prediction of the hypothesis that the conulariid schott was a regular growth feature, produced upon attainment of a certain age (apical retraction hypothesis), is that specimens that preserve their apex (pointed specimens) and belong to taxa that have yielded schott-bearing specimens should exhibit one or more schotts within the test cavity (provided, of course, that such specimens were old enough to form schotts).

Two key predictions of the severance by currents hypothesis are that (1) specimens preserving the apex (and therefore not severed) should not exhibit internal schotts; and (2) percentages of schott-bearing specimens in samples of conulariids should vary significantly, depending on the sedimentology of the deposits hosting the samples. As noted by previous workers (e.g. Barrande 1867; Bouček 1928; Sinclair 1948; Moore *et al.* 1952; Havlíček and Vaněk 1966), conulariids occur in large numbers in a variety of marine strata. These include strata that were deposited under conditions of extremely low physical energy (e.g. dark, laminated, deep-shelf shales and lime mudstones), and strata deposited under conditions of relatively high physical energy (e.g. shallow-shelf quartz sandstones and lime grainstones). If schott formation was associated with severance by currents, then not only should schotts be absent in the test cavity of specimens that were not severed in life, but proportions of schott-bearing specimens should be significantly higher in samples from high-energy deposits than in samples from low-energy deposits (all other factors being equal).

This pattern of occurrence would not be expected were schott formation associated with assumption of a free-swimming mode of life (or, alternatively, if conulariids were pseudoplanktonic organisms that sometimes dropped to the sea floor). This is because schott formation would have been mediated principally by the life history of the developing organism, rather than by physical characteristics of the surrounding water, and because the chances of free-swimming (or pseudoplanktonic) conulariids being preserved in fine grained, low energy deposits, where conulariids commonly occur in great abundance (e.g. Sinclair 1948; Moore *et al.* 1952) and have been found preserved *in situ* (e.g. Rooke and Carew 1983), would have been at least as good as the chances of their being preserved in relatively coarse grained, higher energy deposits. In short, the alternation of generations hypothesis predicts that proportions of schott-bearing specimens in low-versus high-energy deposits should not be significantly different.

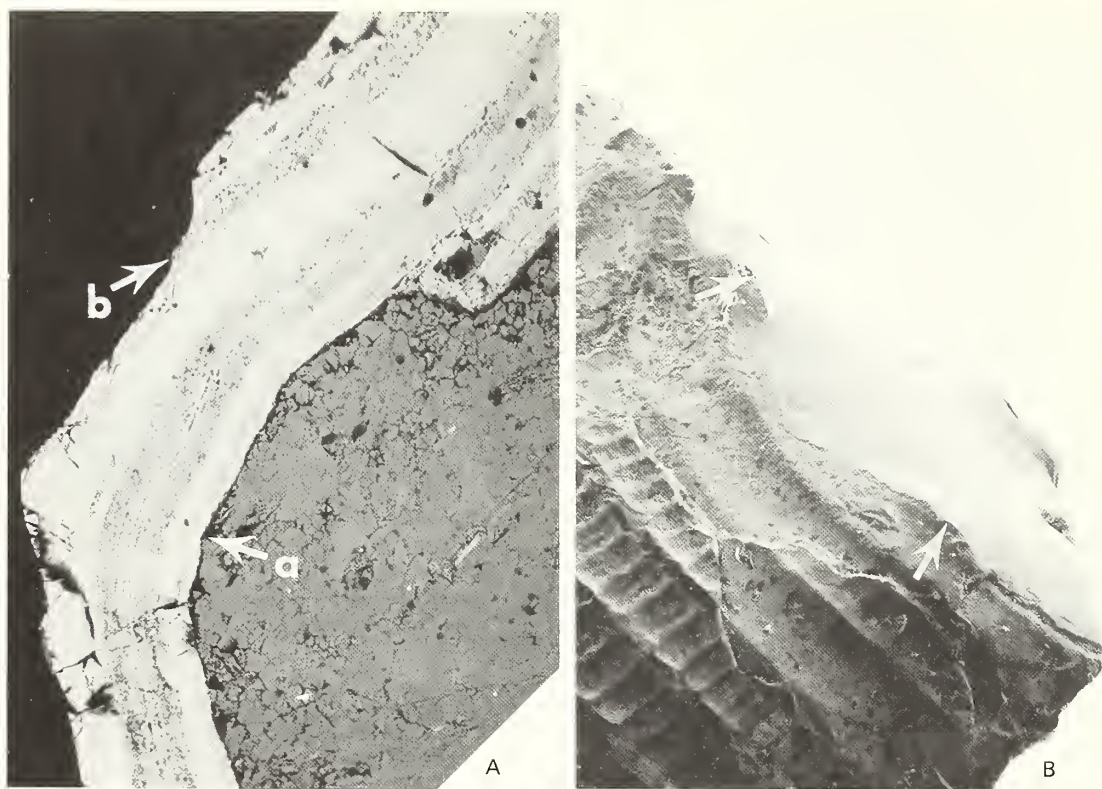
Details of the anatomy of the conulariid schott and schott-bearing conulariids are covered in a Ph.D. dissertation by Sinclair (1948), but this work has not been published. To rectify this deficiency in the conulariid literature, and to present additional information having a potential bearing on alternative interpretations of the cause(s) of schott formation, data on the anatomy of the conulariid schott will be presented in the following section.

Schott-bearing specimens are currently known from five of the twenty-one recognized conulariid genera, namely *Anaconularia* Sinclair, *Archaeoconularia* Bouček, *Conularia* Miller, *Metaconularia* Foerste, and *Paraconularia* Sinclair. The present study is based on direct examination of approximately 1100 specimens of these genera, supplemented by published data on approximately 500 additional specimens. Information on the location of specimens and explanations of repository abbreviations used in the remainder of this paper are presented in the appendices.

ANATOMY OF THE SCHOTT AND SCHOTT-BEARING CONULARIIDS

The conulariid schott is built of numerous, extremely thin (about $1\ \mu\text{m}$), apatitic lamellae, alternatively dense and vacuity-rich, that parallel its surface (Text-fig. 2A). It consists of a transverse portion, or wall, and a longitudinal portion, or sleeve, that extends along the inner surface of the faces proper, toward the aperture. Tracing of schott lamellae in sectioned specimens preserved near their aperture revealed that the sleeve probably extended all the way to the aperture. The wall/sleeve boundary tends to be irregular (Text-fig. 2B), and the surface defined by this boundary may be oriented more or less perpendicular to the test's long axis or inclined at a high angle to it. The wall may be adapically convex, more or less planar, or adaperturally convex. Its surface may be smooth or finely wrinkled, with wrinkles usually concentrated along the wall/sleeve boundary and oriented at various angles to it. In some cases, the wall exhibits a small dimple or dimple-bearing protuberance, usually situated at or near its centre.

As noted by previous investigators (e.g. Barrande 1867; Slater 1907), the distance between the schott and the former apex (estimated by extending the corners of the test to their point of intersection) varies between specimens. For example, in *Conularia trentonensis* Hall (Middle to Upper Ordovician, North America), characterized in life by a maximum test length of at least 10 cm



TEXT-FIG. 2. A, *Conularia trentonensis* Hall; UMMP 7000; Middle Ordovician (Trenton Group); New York, USA; scanning electron photomicrograph of part of a longitudinal section through a terminal schott, showing the finely laminate microstructure, the wall-sleeve junction (arrow labelled 'a'; the sleeve is the portion above the arrow), and the contact between the sleeve and the face proper (arrow labelled 'b') $\times 250$. B, *C. trentonensis* Hall; UMMP 66012; Middle Ordovician (Trenton Group); New York, USA; oblique view of part of the external surface of a terminal schott with a relatively prominent, dimple-bearing protuberance; the wall-sleeve boundary (arrows) is irregular and associated with fine wrinkling of the wall, $\times 22$.

(Van Iten in prep.), schotts occur at test widths ranging from about 1.5 to 6.0 mm ($N = 29$, mean = 3.6 mm, S.D. = 1.1 mm), or from about 10 to 40 mm above the apex.

The cross-sectional geometry of schott-bearing specimens may be more or less rectangular, or strongly rhombic, in some cases to such an extent that members of one pair of opposing corners nearly touch each other (Kiderlen 1937; Sinclair 1948). In specimens showing a strongly rhombic cross section, the schott itself is often smoothly curved and shows no evidence of compactional distortion. This suggests that rhombic specimens terminating in a non-compacted schott exhibited a rhombic cross-sectional geometry while alive (Sinclair 1948).

Although most schott-bearing specimens documented by previous workers (e.g. Barrande 1867; Bouček 1928; Kowalski 1935) exhibit only one schott, some investigators (e.g. Barrande 1867; Slater 1907) maintained that conulariids usually produced multiple schotts. This interpretation was based on the observation that the distance between the schott and the former apex varies between specimens (presumably reflecting post-mortem break-up of specimens), and on the discovery of specimens exhibiting more than one schott. However, present examination of the test cavity of 207 specimens terminating in a schott, including 49 specimens preserving test material (e.g. Text-fig. 1B) and 158 specimens preserved as sandstone steinkerns (Appendix 1), yielded only two specimens,

USNM 373992 (*Conularia quichua* Ulrich) and AMNH 42316 (*C. trentonensis* Hall), having more than one schott (both of these specimens have two schotts, with the second, internal schott situated several millimetres above the terminal one). Previous authors (Steinmann and Döderlein 1890; Slater 1907; Kiderlen 1937; Sinclair 1948) have collectively reported six specimens bearing multiple schotts. Five of these specimens have two schotts, and one of them (Steinmann and Döderlein 1890) has three schotts. These six specimens constitute a very small fraction of the total number (estimated by the present author to be at least 500) of schott-bearing specimens reported by previous authors. Most of these specimens are preserved as sandstone steinkerns or show extensive exfoliation, thus revealing their test cavity. Neither these nor any of the specimens here examined (Appendix 1) exhibit a schott at their apertural end, where one might expect to find a schott (at least occasionally) had conulariids normally produced multiple schotts and undergone break-up. In short, it appears that conulariids almost always produced only one schott.

In specimens having multiple schotts, the sleeve of the schott situated closest to the aperture rests on the inner (adaxial) surface of the sleeve of its neighbour (Sinclair 1948). Together with the observation that schotts are lamellar, with sleeves that extended all the way to the aperture, this suggests that the sequence of formation of multiple schotts was adapertural in direction, and that schotts were produced by centripetal accretion of whole lamellae, along the entire length of the soft body.

OCCURRENCE OF SCHOTTS IN THE TEST CAVITY OF POINTED SPECIMENS

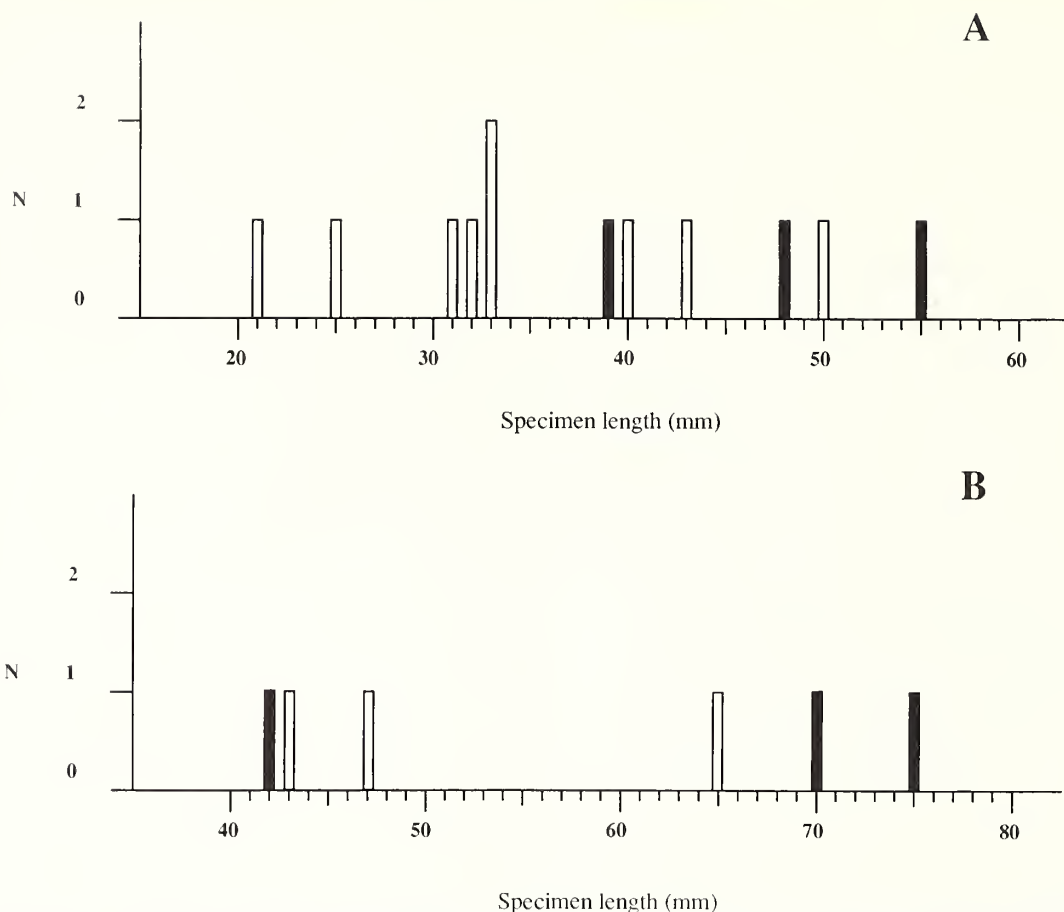
To determine if schotts occur in the test cavity of conulariid specimens that do not terminate in a schott (but that belong to species or genera that have yielded schott-bearing specimens), observations were made on specimens of *Archaeoconularia granulata* (Hall) (Text-fig. 1A; $N = 2$), *Metaconularia manni* (Roy) ($N = 12$), *Conularia splendida* Billings ($N = 9$), *C. trentonensis* Hall ($N = 115$), and several species of *Paraconularia* ($N = 15$) (Appendix 2). Except for certain *Paraconularia* (Appendix 2), all of the 153 specimens in this sample terminate at a test width of 1 mm or less, well below usual levels of occurrence of terminal schotts in conspecific or congeneric, schott-bearing specimens. (Some of the *Paraconularia* terminate at a test width of up to about 5 mm, but this is still below levels of occurrence of terminal schotts in schott-bearing *Paraconularia* specimens here examined.) Most of the specimens (including all *Archaeoconularia granulata* and *Metaconularia manni*, and nearly all *Conularia trentonensis*) are flattened, having been preserved in shale or lime mudstone. For many of these specimens, the presence or absence of internal schotts had to be ascertained by checking for localized deformation of the faces (the test cavity of the remaining specimens has been revealed through exfoliation or sectioning). Two of the species chosen here, *Conularia splendida* and *C. trentonensis*, have yielded schott-bearing specimens. As shown in Text-figure 3, pointed *Conularia* specimens for which reliable estimates of original test length can be obtained fall within or close to the size range of schott-bearing, conspecific specimens whose original test length likewise can reliably be estimated.

None of the specimens in this sample exhibits internal schotts. A similar result was obtained by Barrande (1867), who found that schotts did not occur in the test cavity of several hundred Bohemian specimens, all belonging to genera that have yielded schott-bearing specimens but without a terminal schott themselves. Given that many of the specimens here examined are similar in size to conspecific specimens terminating in a schott (suggesting that the specimens were similar in age), these results tend to falsify the hypothesis that schott production was a regular feature of conulariid ontogeny.

DISTRIBUTION OF SCHOTT-BEARING SPECIMENS RELATIVE TO SEDIMENTARY FACIES

Background

As indicated by studies of the stratigraphy and sedimentology of strata known to bear conulariids (e.g. Branson 1944; Lowenstam 1957; Svoboda 1966; Belt *et al.* 1967; Scoffin 1971; Lane 1973;



TEXT-FIG. 3. A, Histogram showing the estimated original test lengths (as measured along the midlines) of 12 specimens of *Conularia splendida* Billings (Upper Ordovician, northeast Iowa, USA), including 9 pointed specimens (open bars; SUI 49979/3, 61511-61518) and 3 specimens terminating in a schott (solid bars; AC I-1448, SUI 61519-61520). B, Histogram showing the estimated original test lengths (as measured along the midlines) of 6 specimens of *C. trentonensis* Hall (Middle to Upper Ordovician, USA), including 3 pointed specimens (open bars; AMNH 29649, SUI 61506, UWGM WW4001) and 3 specimens terminating in a schott (solid bars; ROM 28324, SUI 61505, UMMP 66012). All of the specimens preserve (or come very close to preserving) their aperture. For all specimens, the position of the apex was estimated by extending the corners to their point of intersection.

Ramsbottom 1973; Bender 1974; Babin *et al.* 1976; Titus and Cameron 1976; Watkins 1978; Titus 1982, 1986; Shaver *et al.* 1986; Williams and Telford 1986; Harland and Pickerill 1982, 1987), conulariids occur in marine deposits spanning a more or less continuous spectrum of shallow nearshore to deep offshore facies. Based on levels of physical energy at the time of deposition, these facies can be interpreted as belonging to one of three general depositional regimes. Arranged in order of increasing energy, these are: (1) sheltered nearshore or deep, distal shelf or basinal waters that were characterized by extremely low physical energy; (2) moderately deep, mesial shelf waters, situated below fair-weather wave base but subject to episodes of relatively high current energy during storms; and (3) shallow, proximal shelf waters, situated closer to fair-weather wave base than Regime 2 settings and subject to more frequent and/or intense episodes of bottom turbulence.

Depositional Regime 1 is represented primarily by dark (grey to black), laminated shales, lime mudstones, and muddy siltstones, commonly with benthic macrofaunas that are sparse and of low diversity. As indicated by faunal and sedimentological evidence and by stratigraphic relationships (e.g. Belt *et al.* 1967; Lane 1973; Mikulic *et al.* 1985a, 1985b; Watkins 1978; Harland and Pickerill 1987), Regime 1 sediments were generally deposited in sheltered lagoons or embayments, or on the distal portions of marine shelves or in cratonic shale basins, below storm wave base.

Conulariids in at least some Regime 1 deposits (e.g. cementstones in the Calciferous Sandstone Group, Lower Carboniferous, Scotland; Belt *et al.* 1967) occur in probable life clusters. In these clusters, which consist of anywhere from 2 to 20 or more specimens, some or all of the specimens converge adapically on a common centre (e.g. Text-fig. 4A; see also discussions and illustrations in Slater (1907), Ruedemann (1925), Sinclair (1940), Lane (1973), and Babcock and Feldmann (1986a, 1986b)). In the remainder of this discussion, such clusters will be referred to as radial clusters.

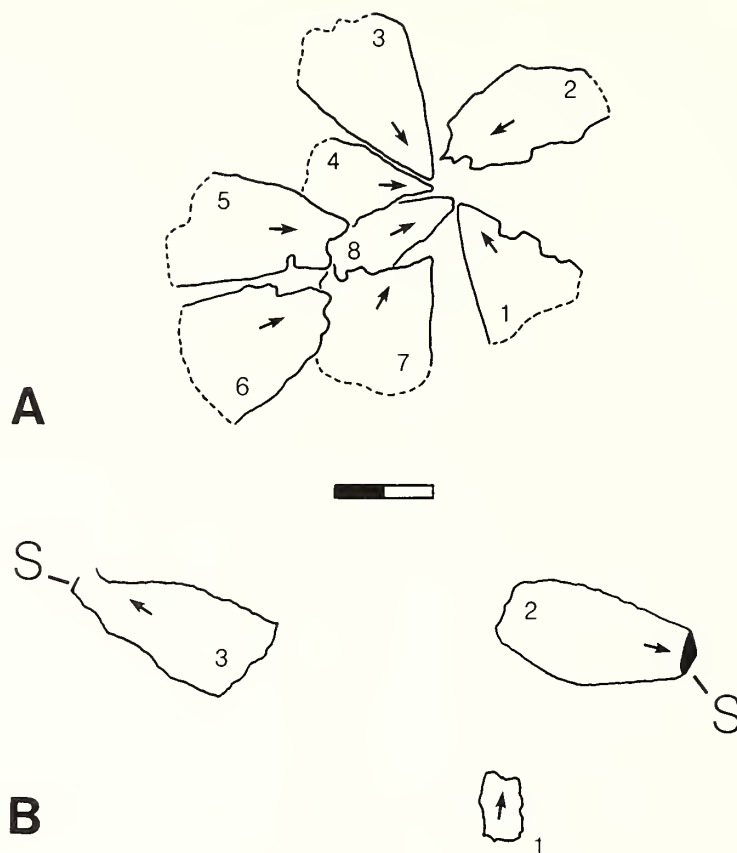
Depositional Regime 2 is represented primarily by light- to dark-coloured, mud-dominated shelf limestones (mudstones and wackestones), with minor amounts of bioclastic limestone, and by interbedded shales and fine sandstones. Faunas in these deposits are more diverse than faunas in Regime 1 deposits, with greater numbers of 'normal' shelf benthos such as articulate brachiopods, bryozoans, and echinoderms. Like conulariids in Regime 1 deposits, conulariids in Regime 2 deposits may be clustered; however, Regime 2 clusters almost never show a radial arrangement (indicating that they have been disrupted; see below). Although Regime 2 deposits contain substantial amounts of mud-sized sediment, suggesting deposition under conditions of low physical energy, episodes of relatively high energy are indicated by the presence of tempestite horizons (e.g. Titus 1982, 1986; Bakush and Carozzi 1986), characterized by sharp (scoured) lower contacts and, in the case of carbonates, packstone to grainstone fabrics (commonly with intraclasts and substantial fragmentation and abrasion of skeletal grains). Clastic analogues of Regime 2 carbonate deposits generally consist of alternating thin shales and fine- to medium-grained, argillaceous or micaceous sandstones (e.g. Havlíček and Vaněk 1966; Bender 1974).

Depositional Regime 3 is represented by thick, laterally extensive deposits of clean, fine- to coarse-grained quartz sandstone, and by carbonate deposits consisting mostly of mud-free, bioclastic limestone, with minor amounts of shale and/or muddy limestone. As indicated by sedimentological and stratigraphic evidence (e.g. Atherton *et al.* 1975; Johnson 1980), the bulk of these units was deposited under conditions of relatively high energy, probably associated with storms.

Clearly, the chances of live conulariids being subjected to current energy of sufficient magnitude to cause breakage would have been greater in Regime 2 or 3 environments than in Regime 1 environments. Thus, if schott formation was associated with repair of a severed apical end, one might expect to observe significantly greater proportions of schott-bearing specimens in Regime 2 and 3 samples than in samples from Regime 1. Since Regimes 2 and 3 were both characterized by episodes of relatively high physical energy (the distinction between these two regimes involving the frequency and intensity of such episodes), differences in the proportion of schott-bearing specimens between samples from Regimes 2 and 3 might not be significant.

Observations

Data on the frequency of occurrence of schott-bearing conulariid specimens in samples from the three depositional regimes outlined above are presented in Table 1. Schott-bearing specimens are extremely rare or absent (only 2 of 688 specimens examined) in samples from Regime 1 deposits, but they are common in samples from Regimes 2 (41 of 75 specimens examined) and 3 (162 of 810 specimens examined). Application of the chi-square statistic indicates that differences in the proportion of schott-bearing specimens between Regime 1 (2/688) and Regimes 2 (41/75) and 3 (162/810), respectively, are highly significant, with the chances that these differences are due to random sampling error being substantially less than 1 in 1000. Similar high confidence levels apply to comparisons involving conspecific specimens or congeneric specimens of very similar species only (see Table 1). (Due to factors associated with sample size, comparisons involving conspecific or



TEXT-FIG. 4. A, *Conularia splendida* Billings; SUI 49979; Upper Ordovician (Maquoketa Formation); northeast Iowa, USA; line drawing of a radial cluster consisting of eight specimens; the arrows indicate the directions in which the apical ends point; scale bar = 2 cm. B, *C. trentonensis* Hall; BMS E10807; Ordovician; New York, USA; line drawing of three specimens preserved on a slab of coarse, skeletal (brachiopod/bryozoan/echinoderm) lime grainstone; two of the specimens terminate in a schott (labelled 'S'). The three specimens are interpreted as members of a single, formerly radial cluster that underwent disruption and transport (see discussion in text).

congeneric specimens only are most appropriately evaluated using Fisher's Exact Test, discussed in detail by Bliss (1967).)

These results are reinforced by semi-quantitative observations on additional samples in the conulariid literature. Kowalski (1935, p. 291), discussing a sample of approximately 20 specimens of *Archaeoconularia pyramidata* (Hoeninghausen) from the Upper May ('*Conularia*') Sandstone (Upper Ordovician), northwest France, states that 'many specimens' terminate in a schott. Bouček (1928, p. 78), who examined approximately 200 specimens of *A. consobrina* (Barrande) from Middle Ordovician quartz sandstones in the Barrandian Basin, Bohemia, reports that 'the apex of the shell is almost always missing, and one finds in its place a hemispherical [schott]'. Barrande (1867, p. 15), commenting on Barrandian Basin conulariids in general (a sample consisting of several thousand specimens), notes that 'in most species, especially those that [occur] in shales, we see conulariids terminating in a sharp point...[but] five of our species, preserved in quartzite..., show, in many cases, a [schott]'. Similarly, Slater's (1907) data on the anatomy of British conulariids indicate that whereas conulariids from shallow-water, open shelf limestones (e.g. the Silurian Wenlock Limestone

Species	Unit and Age	Locality	Host Lithology	N	Ns	Np
Depositional Regime 1						
<i>Archaeoconularia</i>						
(1) <i>A. exquiritia</i> **	Middle Ordovician (1)	Bohemia	Dark shale	200	0	?(*)
<i>Conularia</i>						
(2) <i>C. trentonensis</i>	Collingwood Shale (U. Ordo., 2)	Ontario	Black, laminated shale	40	2	38
(2) <i>C. trentonensis</i> ++	Tetereauville Fm. (M. Ordo., 3)	Quebec	Black, laminated lime mudstone	100	0	?(*)
(2) <i>C. trentonensis</i>	Brandon Bridge Fm. (Silur., 4)	Wisconsin	Grey, laminated shale	159	0	113
<i>Metaconularia</i>						
(3) <i>M. aspersa</i>	Lower Ludlow Shale (Silur., 5)	England	Grey-brown, laminated shale	3	0	2
(3) <i>M. bilineata</i> **	Liten Fm. (Silur., 6)	Bohemia	Black, laminated calcareous shale	17	0	?
(3) <i>M. manni</i>	Lecthaylus Shale (Silur.)	Illinois	Grey, laminated shale	13	0	12
<i>Paraconularia</i>						
(4) <i>P. chagrinensis</i>	Chagrin Shale (U. Devon.)	Ohio	Grey, laminated shale	13	0	2
(4) <i>P. chesterensis</i> *	Edwardsville Mbr., Muldraugh Fm. (Miss., 7)	Indiana	Grey, laminated shaley siltstone	53	0	?(*)
(4) <i>P. tenuis</i> +	Cementstone Facies, Calcareous Sandstone Gp. (Miss., 8)	Scotland	Grey, laminated lime mudstone	70	0	?(*)
Depositional Regime 2						
<i>Conularia</i>						
(5) <i>C. sowerbyi</i>	Wenlock Limestone (Silur., 9)	England	Lime mudstone/wackestone	25	14	0
(6) <i>C. subcarbonaria</i>	Keokuk Limestone (Miss., 10)	Illinois	Lime wackestone/packstone/grainstone	10	5	0
(6) <i>C. subcarbonaria</i>	Ramp Creek Mbr., Harrodsburg Limestone (Miss., 11)	Indiana	Lime wackestone/packstone	1	0	0
(7) <i>C. trentonensis</i>	Verulam Fm. (M. Ordo., 2)	Ontario	Lime wackestone/packstone/grainstone	11	5	0
(7) <i>C. trentonensis</i>	Denley, Kings Falls, Sugar River Fms. (M. Ordo., 12)	New York	Lime wackestone/packstone/grainstone	11	6	0
(7) <i>C. trentonensis</i>	Sherwood Mbr., Dunleith Fm. (M. Ordo., 13)	Iowa	Lime wackestone/packstone	8	2	0
<i>Metaconularia</i>						
(8) <i>M. calderi</i>	Verulam (Cobourg) Fm. (M. Ordo., 2)	Ontario	Lime wackestone/packstone/grainstone	3	3	0
(8) <i>M. divisa</i>	Dubuque Fm. (U. Ordo., 13)	Iowa	Lime mudstone/wackestone	5	5	0
(8) <i>M. sp.</i>	Lower Lindsay Fm. (M. Ordo., 14)	Ontario	Lime wackestone/packstone	1	1	0
Depositional Regime 3						
<i>Anaconularia</i>						
(9) <i>A. anomala</i>	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium, micaceous quartz sandstone	760	140	0
<i>Archaeoconularia</i>						
(10) <i>A. consobrina</i>	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium, micaceous quartz sandstone	10	5	0
(10) <i>A. pyramidata</i>	Upper May (<i>Conularia</i>) Sandstone (U. Ordo., 15)	Brittany	Fine to coarse quartz sandstone	20	10	0
<i>Conularia</i>						
(11) <i>C. subcarbonaria</i>	Burlington Limestone (Miss., 16)	Missouri	Coarse, skeletal lime grainstone	11	3	0
(12) <i>C. trentonensis</i>	Ordovician	New York	Coarse, skeletal lime grainstone	3	2	0
<i>Paraconularia</i>						
(13) <i>P. sp.</i>	Burlington Limestone (Miss., 10)	Iowa	Coarse, skeletal lime grainstone	5	2	0
(13) <i>P. sp.</i>	Glen Dean Limestone (Miss., 11)	Indiana	Coarse, skeletal lime grainstone	1	0	0

TABLE 1. Frequency of occurrence of schott-bearing conulariid specimens in samples from the three depositional regimes outlined in the text. Lettered symbols are as follows: N = number of specimens; Ns = number of specimens terminating in a schott; Np = number of pointed specimens (specimens tapering to a width of 1 mm or less and lacking a terminal schott). Sources of numerical data taken from the literature are as follows: ** = Bouček (1928); ++ = Sinclair (1948); * = Lane (1973); + = Slater (1907). An asterisk following a question mark in the Np column indicates that the percentage of pointed specimens is reported to be large. Numbers following the geologic age of the host rock unit refer to one of the following sedimentological and/or stratigraphic studies: 1, Havlíček and Vaněk (1966); 2, Brett and Brookfield (1984); 3, Harland and Pickerill (1982); 4, Mikulic *et al.* (1985a, 1985b); 5, Watkins (1978); 6, Svoboda (1966); 7, Lane (1973); 8, Belt *et al.* (1967); 9, Scoffin (1971); 10, Atherton *et al.* (1975); 11, Shaver *et al.* (1986); 12, Titus (1982, 1986) or Titus and Cameron (1976); 13, Bakush and Carozzi (1986); 14, Williams and Telford (1986); 15, Babin *et al.* (1976); 16, Branson (1944). See Appendix 3 for information on specimen locations. Numbers in parentheses preceding species names designate samples used in statistical analysis. Conspecific specimens from different localities but similar deposits were combined into one sample. In some cases, congeneric specimens from the same depositional setting were also combined to form a single sample (to compensate for small numbers of specimens and/or restriction of species to a single depositional setting). Statistical analysis was conducted on the following sample pairs: 1–4 vs 5–8; 1–4 vs 9–13; 1 vs 10; 2 vs 5; 2 vs 6; 2 vs 7; 2 vs 11; 2 vs 12; 3 vs 8; 4 vs 13.

(Scoffin 1971) and the Carboniferous Limestone (Ramsbottom 1973)) often terminate in a schott, conulariids from dark, graptolitic slates and shales, deposited in settings further offshore (Rayner 1967), do not exhibit a schott but commonly taper to a point.

Discussion

The foregoing results falsify the hypothesis that schott-bearing conulariids were similar to scyphozoan medusa, but they are consistent with the hypothesis that schott-bearing conulariids represent living individuals severed by currents. Additional lines of evidence suggest that patterns of occurrence observed here are not the result of other causes, for example mass mortality of very young conulariids (killed before they had the chance to form schotts), or inhibition of schott formation by other factors of the local environment (e.g. low dissolved oxygen content). Although many of the conulariids examined here have been broken well below the aperture (making it impossible to obtain reliable measurements of the original size of these specimens), those Regime 1 specimens that are more or less intact are generally similar in size to conspecific or congeneric, schott-bearing specimens from Regime 2 and 3 deposits, and thus it seems unlikely that low frequency of occurrence of schott-bearing specimens in Regime 1 samples is due to unusually early death. This conclusion is reinforced by data in Barrande (1867) indicating that Bohemian *Archaeoconularia* (Table 1) from dark shales (Regime 1) are about as large as morphologically similar, schott-bearing *Archaeoconularia* collected from quartz sandstones (Regimes 2 and 3). Together with the observation that Regime 1 specimens here examined show no other evidence of abnormal development (e.g. departure from patterns of test ornamentation exhibited by specimens from Regime 2 or 3 deposits), these observations also tend to rule out the hypothesis that low frequency of occurrence of schott-bearing specimens in Regime 1 deposits is due to inhibition of schott formation by unfavourable environmental conditions.

Data obtained at finer scales of observation lend additional support to the hypothesis that schott formation was prompted by severance. For example, the one Regime 1 sample here encountered that contains schott-bearing specimens (*Conularia trentouensis* Hall, Collingwood Shale; 2 schott-bearing specimens out of 40 specimens sampled) appears to differ from several other Regime 1 deposits in lacking radial clusters. This suggests that Collingwood conulariids were subjected to some degree of disturbance, possibly associated with storm events affecting adjacent, shallower-water shelf environments (Brett and Brookfield 1984).

Evidence of disturbance is exhibited by many of the conulariids from Regimes 2 and 3. Conulariid steinkerns consisting of quartz sandstone often contain large amounts of medium to coarse sand (see also Kowalski 1935), suggesting that the horizons that yielded these specimens were deposited under conditions of relatively high energy. Similarly, most of the schott-bearing specimens from Regime 2 carbonates occur in a wackestone or packstone matrix rich in disarticulated echinoderm ossicles and disarticulated and/or broken trilobites and brachiopods, suggesting that they were collected from tempestite horizons. At least five of the schott-bearing specimens examined here occur in non-radial clusters (e.g. Text-fig. 4B). The three-specimen cluster shown in Text-figure 4B, which includes two specimens terminating in a schott, occurs in coarse, bioclastic limestone. Conulariids in the units from which this and similar clusters were collected are so rare (Van Iten in prep.) that it seems extremely unlikely that they are artefacts of concentration by currents or scavengers. Rather, they seem best interpreted as former life clusters. Coupled with sedimentological evidence indicating current action, the present non-radial arrangement of specimens in these clusters suggests that they were physically disrupted. As expected, schott-bearing specimens do not occur in currently known radial clusters (Van Iten in prep.), which have undergone little or no disruption.

CONCLUSION

Analyses of the anatomy and patterns of occurrence of the conulariid schott show that schotts do not occur in the test cavity of specimens that lack a terminal schott and are preserved close to the apex, and that schott-bearing conulariids occur in significantly higher proportions in samples from

high-energy deposits than in samples from low-energy deposits. These results corroborate the hypothesis that schott-bearing conulariids represent living individuals severed by currents, but they are inconsistent with other previously suggested interpretations of schott-bearing conulariids. The occurrence of specimens having more than one schott, interpreted by some investigators (e.g. Hall 1847) as evidence that schott formation was a regular feature of conulariid ontogeny, is not necessarily inconsistent with the hypothesis that schott-bearing conulariids were severed in life. As an example, severed individuals may have been susceptible to infection or necrosis, leading to additional episodes of schott formation.

Certainly, previously offered interpretations of schott-bearing conulariids do not exhaust the full array of interpretations that might reasonably be suggested by analogy with living organisms. However, none of these interpretations (e.g. obligatory decollation of the apical end, encystment) appears to carry with it the expectation that schott-bearing conulariids should occur in significantly higher proportions in high-energy deposits than in low-energy deposits.

Although schott-bearing specimens probably were not medusa-like, as held by Kiderlen (1937) and several other proponents of a scyphozoan affinity for conulariids, this does not necessarily mean that conulariids did not produce medusae (through means other than direct transformation of test-bearing, polypoid individuals; e.g. Van Iten 1989, 1991*b*). Moreover, even if conulariids did not produce medusae, this alone would not mean that conulariids and scyphozoans were not closely related to each other, since some scyphozoans lack a medusa (Hyman 1940).

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APPENDICES

The following three appendices list conulariid specimens used as data in the present study. Abbreviations of repositories housing these specimens are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; BM-UW, Burke Museum, University of Washington, Seattle; BMS, Buffalo Museum of Science, Buffalo; BUGM, Birmingham University Geology Museum, Birmingham; CM, Carnegie Museum of Natural History, Pittsburgh; CMNH, Cleveland Museum of Natural History, Cleveland; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; ISGS/ISM, Illinois State Geological Survey/Illinois State Museum, Champaign/Urbana; IUPC, Indiana University, Paleontological Collections, Bloomington; NYSM, New York State Museum and Science Service, Albany; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMP*, University of Montana Museum of Paleontology, Missoula; USNM, United States National Museum, Washington; UWGM, University of Wisconsin Geological Museum, Madison.

APPENDIX 1

List of conulariid specimens terminating in a schott and examined for the presence of schotts within the test cavity. Species followed by an asterisk are preserved as sandstone steinkerns. N = number of specimens examined.

Species	Repository	N
<i>Anaconularia anomala</i> * (Barrande)	MCZ	144
<i>Archaeoconularia consobrina</i> * (Barrande)	MCZ	5
<i>A. dubia</i> (Sinclair)	ROM 18889	1
<i>A. pyramidata</i> * (Hoeninghausen)	FMNH PE294, PE379-382; GSC 87183; ROM 22289, 22532	9
<i>Conularia multicostata</i> Meek and Worthen	AC I4160, I4164	2
<i>C. quichua</i> Ulrich	USNM 373992	1
<i>C. sp.</i>	UMMP 259	1
<i>C. sp.</i>	ISGS/ISM 4434	1
<i>C. sp.</i>	SUI 62675a	1
<i>C. splendida</i> Billings	SUI 61519-61520	2
<i>C. subcarbonaria</i> Meek and Worthen	FMNH UC18494, UC19647; ISGS/ISM 2609; MCZ 27951, 27954-27955	7
<i>C. trentonensis</i> Hall	AMNH 29650, 42316; BMS 10804; NYSM 3492; ROM 67, 23278, 23737, 23738, 24007, 28324, 24917; SUI 61502; UMMP 66012-66016; UMPC W1991	25
<i>Metaconularia calderi</i> Sinclair	GSC 9794-9795	2
<i>M. sp.</i>	ROM 87DR	1
<i>M. divisi</i> Sinclair	SUI 53089, 62678-62679	3
<i>Paraconularia byblis</i> (White)	UMMP 2167	2

APPENDIX 2

List of conulariid specimens not terminating in a schott and examined for the presence of schotts within the test cavity. The letter P following a specimen number or numbers indicates that the corresponding specimen or specimens taper to a test width of 1 mm or less.

Species	Repository
<i>Archaeoconularia granulata</i> (Hall)	AMNH 791(P) (2 specimens)
<i>Conularia splendida</i> Billings	SUI 499793(P) (1 specimen), SUI 61511–61518(P) (8 specimens)
<i>C. trentonensis</i> Hall	AMNH 29649(P) (1 specimen); SUI 61506 (1 specimen); UWGM WW4001(P) (113 specimens)
<i>Metaconularia manni</i> (Roy)	FMNH PE6252–6256(P), PE10132(P), PE23674–23675(P), unnumbered(P) (12 specimens)
<i>Paraconularia chagrinensis</i> Babcock and Feldmann	CMNH 1788(P), 6633 (3 specimens)
<i>P. chesterensis</i> (Worthen)	GSC 49383 (1 specimen)
<i>P. recurvatus</i> Babcock and Feldmann	USNM 409806 (1 specimen)
<i>P. subulata</i> (Hall)	CM 34521, 34524 (2 specimens); CMNH 1788, 6633 (3 specimens); UMMP* 5613A/I7106, 5628NC/MI7106 (2 specimens)
<i>P. yochelsoni</i> Babcock and Feldmann	UMMP 45499(P), 45500(P) (3 specimens)

APPENDIX 3

Specimen numbers for samples listed in Table 1.

Species	Repository
Depositional Regime 1	
<i>Comularia</i>	
<i>C. trentonensis</i> Hall (Collingwood Fm.)	ROM 27274 (40 specimens)
<i>C. trentonensis</i> Hall (Brandon Bridge Fm.)	UWGM WW4001 (159 specimens)
<i>Metaconularia</i>	
<i>M. aspersa</i> (Slater)	BMNH G4603, G5373, G12879 (3 specimens)
<i>M. mami</i> (Roy)	FMNH PE6252–6256, PE10132, PE23674–23975, FMNH unnumbered (13 specimens)
<i>Paraconularia</i>	
<i>P. chagrinensis</i> Babcock and Feldman	CMNH 1247, 1272, 1427, 1622, 1674, 1788, 1818, 4030, 4292, 6633, 6717, 6807–6808 (13 specimens)
Depositional Regime 2	
<i>Comularia</i>	
<i>C. sowerbyii</i> (Slater)	BMNH 6275, 6327, 10043, 11795, 17500–17505, unnumbered (14 specimens); UBGm 'Holcroft Pteropoda' (10 specimens)
<i>C. subcarbonaria</i> (Meek and Worthen)	FMNH UC18494, UC19647, FMNH unnumbered (8 specimens); ISGS/ISM 2609 (1 specimen); ISM 2609 (1 specimen); IUPC 17482 (1 specimen)
<i>C. trentonensis</i> Hall (Verulam Fm.)	ROM 67, 23738 (512T), 24917 (24OU) (9 specimens); GSC 1725–1726 (2 specimens)
<i>C. trentonensis</i> Hall (Denley Fm.)	UMMP 66012–66022 (11 specimens)
<i>C. trentonensis</i> Hall (Sherwood Mbr.)	SUI 61502–61505 (8 specimens)
<i>Metaconularia</i>	
<i>M. calderi</i> Sinclair	GSC 9794–9795 (2 specimens); Sinclair (1940, pl. 3, figs 3–5; 1 specimen)
<i>M. divisa</i> Sinclair	BM-UW (2 specimens); SUI 53089, 62678–62679 (3 specimens); UMPC W1994 (3 specimens); Sinclair (1948, pl. 8, figs 12–14; 1 specimen)
<i>M. sp.</i>	ROM 87DR (1 specimen)
Depositional Regime 3	
<i>Anaconularia</i>	
<i>A. anomala</i> (Barrande)	MCZ (760 specimens)
<i>Archaeoconularia</i>	
<i>A. consobrina</i> (Barrande)	MCZ (10 specimens)
<i>A. pyramidata</i> (Hoeninghausen)	BMNH 3408–3409 (9 specimens); FMNH PE294, PE379–382, FMNH unnumbered (7 specimens); GSC 87180 (1 specimen); ROM 22289, 22532 (3 specimens)
<i>Comularia</i>	
<i>C. subcarbonaria</i> Meek and Worthen	MCZ 27946–27956 (11 specimens)
<i>C. trentonensis</i> Hall	BMS E10807 (3 specimens)
<i>Paraconularia</i>	
<i>P. sp.</i>	USNM 57164, 99502 (4 specimens); ISGS (ISM) 10742 (4291) (1 specimen); IUPC 6071 (1 specimen)

HENSONELLA DINARICA, AN ORIGINALLY CALCITIC EARLY CRETACEOUS DASYCLADACEAN ALGA

by M. D. SIMMONS, D. EMERY and N. A. H. PICKARD

ABSTRACT. *Hensonella dinarica* (Radoičić) is an Early Cretaceous, Tethyan microfossil, considered to be either a dasycladacean alga or a problematicum. This is because its preservation in yellowish radial calcite is highly unusual for dasycladacean algae, which are typically preserved in drusy calcite replacing the original aragonite. Petrological, cathodoluminescence and chemical microprobe studies of specimens of *H. dinarica*, principally from the Middle East, suggest that the original mineralogy of this microfossil was calcitic. The morphology of this species is suggestive of a dasycladacean alga, and so it is considered to be an originally calcitic dasycladacean alga, an unusual phenomenon.

HENSONELLA DINARICA (Radoičić) is a microfossil which is often found in shallow water, Early Cretaceous (Hauterivian–late Aptian), Tethyan sediments, particularly those of the Middle East and Mediterranean regions (Bassoulet *et al.* 1978; Simmons 1990). The species is most typical of the Barremian–Aptian period in southern Tethys. Although originally considered to be a dasycladacean alga (*Salpingoporella dinarica* Radoičić, 1959), other authors have questioned this taxonomic assignment (usually with reference to *Hensonella cylindrica* Elliott, 1960, junior synonym of *S. dinarica*), because of the unusual preservation of specimens of this species. In thin-section it is typically preserved in fibrous, radial calcite with a yellowish tint and has a dark, micritic, inner layer to the calcitic wall (Text-fig. 1A–C). Dasycladacean algae usually have an originally aragonitic mineralogy which is replaced by drusy calcite during diagenesis (Wray 1977). The preservation of *H. dinarica* suggests an originally calcitic mineralogy. In order to determine its original mineralogy, conventional transmitted light and cathodoluminescence petrography have been employed, together with microchemical techniques using an electron microprobe.

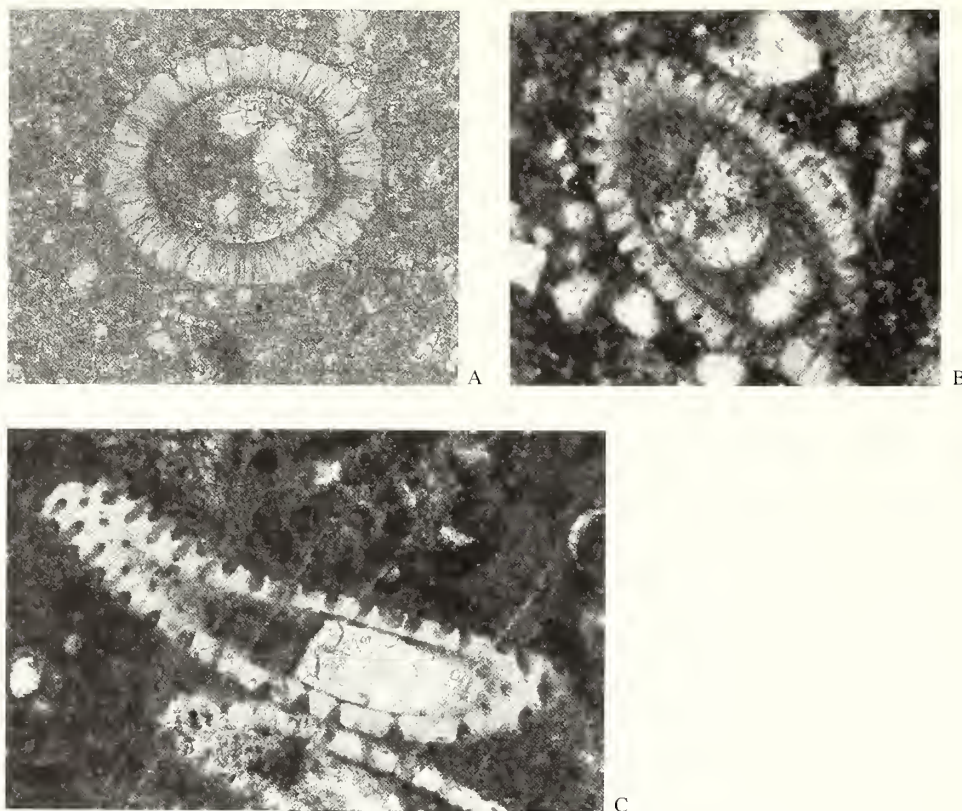
TECHNIQUES AND RESULTS

The main specimens examined in this study are from the Early Cretaceous Kahmah Group (Glennie *et al.* 1974) of the Oman Mountains, notably the Late Barremian and Early Aptian Kharaib and Shuaiba Formations. For further details of associated fauna, flora and sedimentology see Simmons and Hart (1987), Hughes Clarke (1988) and Simmons (1990).

Topotype specimens of *S. dinarica* from the Early Cretaceous sediments of the Dinarides, Yugoslavia, were kindly made available by Dr M. A. Conrad. The type specimens of *H. cylindrica* from the Early Cretaceous sediments of the Middle East were studied at the British Museum (Natural History), and additional material from the Middle East and the Mediterranean was studied from the reference collections of the BP Research Centre, Sunbury-on-Thames.

In addition to conventional transmitted light petrography, cathodoluminescence petrography and microchemical techniques were used to ascertain the present and original mineralogy of *H. dinarica*. Polished thin-sections containing the microfossil were examined firstly in cathodoluminescent light (Marshall 1987) for evidence of diagenetic alteration (Popp *et al.* 1986). Neither the algae nor surrounding calcite matrix and cement luminesced in any of the samples examined. This indicates that the algae had not been replaced by luminescent calcite, but it is not unequivocal evidence of a primary calcite mineralogy.

The same samples examined in cathodoluminescent light were analysed on an electron microprobe for



TEXT-FIG. 1. A–C, *Hensonella dinarica* (Radoičić). A, WG23; Early Aptian, Shuaiba Formation; Oman; transverse section showing inner micritic wall and radial calcitic structure, $\times 80$. B, WM105; Hauterivian–Barremian, Kharab Formation; Oman; transverse section showing radial structure and dasycladacean verticils, $\times 80$. C, RR019440/A309; Barremian–Aptian; Zeta Plain, Yugoslavia; oblique transverse section of a topotype of *Salpingoporella dinarica* Radoičić, showing dasycladacean verticils and faint radial calcitic structure, $\times 60$. Specimens WG23 and WM105 are held in the Biostratigraphy Reference Collection, BP Research Centre, Sunbury-on-Thames, UK; specimen RR018440/A309 is held in the collection of Petroconsultants, Geneva, Switzerland.

residual strontium and magnesium. High concentrations of strontium normally indicate a precursor aragonite mineralogy (Sandberg 1985). Modern aragonitic algae contain up to several hundred to a few thousand ppm strontium. High concentrations of magnesium, which may be sited in microdolomites (Lohmann and Meyers 1977; Meyers 1978) after diagenetic alteration, are indicative of an originally high magnesium calcite mineralogy.

The microprobe analyses of specimens of *H. dinarica* were obtained on a Cameca Camebax Microbeam system, operating with an accelerating voltage of 20 kV and beam current of 10 nA and a count time of 30 sec. The beam was rastered over a $7.5 \mu\text{m}$ square to reduce volatilization of CO_2 . Twenty-three spot analyses were made of three samples. Four spot analyses were also made of the calcite cement. In addition to the spot analyses, a line scan was made across one alga and through the surrounding cement. Table 1 summarizes the microprobe results.

The analyses show the alga to be composed of low magnesium calcite (i.e. $< 4 \text{ mole } \% \text{ MgCO}_3$). There is no evidence for high concentrations of strontium or magnesium in any portion of the alga. It is impossible to rule out completely a high magnesium calcite precursor, because high magnesium calcite can lose magnesium without any discernible petrographic change (Friedmann 1964; Towe and Hemleben 1976). Moreover, the magnesium levels recorded in *H. dinarica* (Table 1) are not atypical of those quoted for original high

TABLE 1. Magnesium and strontium content of algae and cement from microprobe spot analyses.

	mole % MgCO ₃	Sr (ppm)	N
Specimen 1	1.10	508	9
Specimen 2	1.14	431	9
Specimen 3	1.05	321	5
Average	1.14	437	23
Calcite cement	1.16	523	4

magnesium calcite cements which have converted to diagenetic low magnesium calcite (e.g. see values quoted in Lochmann and Meyers 1977; Davies 1977; Marshall and Ashton 1980; Videtich 1985; Saller 1986; Carpenter and Lohmann 1989; Mazzullo *et al.* 1990). However, the algae lack microdolomite inclusions which are commonly formed during the stabilization of high magnesium calcite (cf. Lohmann and Meyers 1977; Davies 1977; Meyers 1978; Carpenter and Lohmann 1989). Combined with the lack of replacement by drusy calcite and albeit equivocal luminescence evidence, this strongly suggests that the alga had an originally calcitic and probably low magnesium calcite mineralogy. The radial fibrous calcite of the thallus and its dark inner micritic layer are hence interpreted as representing the primary mineralogy of *H. dinarica*.

DISCUSSION

Previous interpretations

Hensonella dinarica was first described by Radoičić (1959), from Early Cretaceous sediments of the Dinarides, Yugoslavia, in the genus *Salpingoporella*, and considered to be a dasycladacean alga. Independently, Elliott (1960) described *H. cylindrica* from the Early Cretaceous of the Middle East, and from its preservation (see below) classified it as a problematicum, probably a scaphopod. Most subsequent workers, including Elliott (1968; pers. comm. 1988), have agreed that *H. cylindrica* is a junior synonym of *S. dinarica*. Johnson (1969) argued that the distinctive preservation of *H. cylindrica* is not seen in *S. dinarica* and kept the two species separate: *H. cylindrica* being a problematicum, *S. dinarica* a dasycladacean alga. However, Elliott (1968, p. 77) still expressed doubts about its algal origin: 'In conclusion, I consider this organism is best classified as a problematicum'. In contrast to this, Bassoullet *et al.* (1978), Conrad (pers. comm. 1988) and Radoičić (pers. comm. 1988) are in no doubt that *S. dinarica* and *H. cylindrica* are synonyms and refer to a dasycladacean alga.

Luperto Sinni and Masse (1982, 1984, 1986) placed *S. dinarica* in synonymy with *H. cylindrica*, but under the generic name *Hensonella* in recognition of its unusual preservation. Like Elliott (1968), they suggested (although did not demonstrate) that *H. dinarica* was originally calcitic. Furthermore, they considered it to be originally high magnesium calcite, although admitting that this was difficult to determine on petrological characteristics alone. The microprobe results presented herein suggest that the species was originally formed of low magnesium calcite. Luperto Sinni and Masse (1982) suggested that the species might be typical of inner shelf environments with high salinities, 'continental influence' and fluctuations in the Mg/Ca ratio. In support of this, they noted that Jaffrezo and Renard (1979) suggested that *Zergabriella embergeri* (Bouroullec and Deloffre) and *Clypeina jurassica* Favre, species also considered by Luperto Sinni and Masse (1982) to be originally calcitic, were typical of similar inner shelf conditions. However, our studies suggest that *H. dinarica* can be found in a variety of shelf environments and is not particularly indicative of hypersaline inner shelf conditions.

Morphological characteristics

The reasons for the uncertainty over the taxonomic position of *H. dinarica* centre around the crystalline structure of the thallus wall as alluded to by Radoičić (1959), and more fully discussed by Elliott (1960). Three features are noticeable: (i) the wall appears to be formed of radial, fibrous

calcite, (ii) this has a yellowish or honey coloured tint, (iii) a dark, inner micritic layer to the thallus is typically present. These features are unusual for a dasycladacean alga, and were used by Elliott (1960, 1968) to argue for a non-algal origin for this fossil. Typical *Salpingoporella*, and other dasycladaceans, have a thallus wall composed of drusy, unstructured calcite, replacing the original aragonite. Elliott (1968) was the first to suggest that the preservation of *H. dinarica* related to an original, organically formed, calcite structure. Luperto Sinni and Masse (1982) also agreed with this interpretation, while Bassoullet *et al.* (1978) and Radoičić (1959) placed little significance in the form of preservation, arguing that the radial structure originates from diagenetic alteration. Our results confirm the assertion of Elliott (1968) that *H. dinarica* was originally calcitic.

Examination of the type figures of *S. dinarica* and *H. cylindrica* strongly suggests that the two species are synonymous. This is confirmed by comparison of topotypes of *S. dinarica* and the syntypes of *H. cylindrica*. As stated by Elliott (1968, p. 76) 'Slight differences in the two authors' descriptions can be reconciled by examination of large sets of specimens'.

Specimens described as *S. dinarica* and *H. cylindrica* show considerable variability, not only in the nature of the wall, but also in terms of morphology. Some topotype specimens of *S. dinarica* clearly show a fibrous, radial wall, whilst in others this is poorly developed. The topotypes do not show a particularly strong yellowish tint, as do the syntypes of *H. cylindrica*. More importantly, the topotype specimens of *S. dinarica* (and indeed the holotype illustrations) resemble dasycladacean algae, especially the genus *Salpingoporella*. Features typical of dasycladacean algae are not clear in the syntypes of *H. cylindrica*, but as noted and illustrated by Elliott (1968), they do occur 'not uncommonly' in Middle eastern specimens referred to *H. cylindrica*. This is confirmed by examination of specimens from the Kahmah Group of the Oman Mountains. Much of the morphological variation associated with this species can be attributed to preservation problems (erosion, etc.), and variability with depth and orientation of thin section.

Of particular note is the presence of 'pores' which are regularly spaced, alternating in position through progressively higher levels in the thallus. These can be interpreted as verticils of lateral branches (see Elliott 1968, plate 22, fig. 2; Text-fig. 1c). Overall the morphology is closely comparable with that of *S. muehlbergii* (Lorenz), the type species of *Salpingoporella*. The thallus is unsegmented with a wide axial hollow and only primary branches are present. The dark inner micritic layer to the thallus wall (thickness 0.012–0.018 mm) can be interpreted as being the preserved organic membrane lining the main axis of the thallus. Elliott (1968) noted that crushed specimens are still held together by this layer, suggesting that it had an original organic nature with some flexibility.

Other records of algae which show all the features of dasycladaceans, but are considered to be originally calcitic include the Visean 'dasycladacean' alga, *Koninckopora* (Wright 1981). This fossil is preserved in very fine-grained, sometimes acicular calcite. Like *H. dinarica*, *Koninckopora* often displays a micritic lining to the thallus wall. Other possible examples include the Late Jurassic species *Salpingoporella sellii* (Crescenti) and *Griphoporella? minima* Nikler and Sokač, both sometimes preserved in fine radial calcite. Elliott (1963) considered that *Pseudovermiporella* Elliott, a questionable Permian dasycladacean, was of calcitic origin. Some species of the Late Jurassic–Early Cretaceous dasycladacean *Zergabriella embergeri* display fibro-radial walls with a yellowish tint and a micritic inner layer to the thallus wall, as in *H. dinarica* (see illustrations in Granier 1989). Further research is needed to establish how well developed is this feature in this species, and if it relates to an original calcitic mineralogy as suggested by Luperto Sinni and Masse (1982). These authors also considered *Chypeina jurassica* to be originally calcitic, and (Luperto Sinni and Masse 1984, 1986) placed *Salpingoporella urladanasi* Conrad, Peybernes and Radoičić in the genus *Hensonella* on account of its similar preservation to *H. dinarica*, but differing in its larger dimensions.

Thus whilst the majority of fossil dasycladaceans were originally aragonitic, there may have been a few taxa which were originally calcitic. Pending further research to establish the number of calcitic 'dasycladaceans', and the reasons for their unusual mineralogy, no new suprageneric taxonomic group is established here. Interestingly, the majority of occurrences of possible originally calcitic 'dasycladaceans' is within the Late Jurassic–Early Cretaceous and Early Carboniferous. These were

periods when, according to Sandberg (1983), non-skeletal carbonates were dominated by calcite rather than aragonite ('aragonite inhibiting episodes'). These may have been brought about by plate-tectonically influenced oscillations in the vapour pressure of CO₂, which in turn correlate with other known global oscillations in eustacy and climate. However, it should be stated that originally aragonitic dasycladaceans are also abundant during these periods, and it is uncertain whether the occurrence of originally calcitic dasycladaceans can simply be attributed to an 'aragonite inhibiting' process.

It is worth noting that other mineral phases besides aragonite are known within dasycladaceans. For example, calcium oxalate has been recorded in reproductive discs of *Acetabularia* (Elliott 1979).

CONCLUSIONS

The preservation of *H. dinarica* relates to a primary organic calcitic mineralogy, although the morphology of the species is in keeping with the dasycladacean genus *Salpingoporella* Pia. Such an original mineralogy is almost unique in the family Dasycladaceae where primary mineralogy is normally aragonitic (Wray 1977). In fossils this is usually replaced by drusy calcite. The genus *Hensonella* Elliott is therefore retained to identify originally calcitic homeomorphs of *Salpingoporella*. Further research is in progress which may lead to the identification of other originally calcitic 'dasycladacean' taxa. If further taxa are identified, it may be necessary to erect a new suprageneric group to accommodate such forms (e.g. 'Hensonellaceae'), or to amend the diagnosis of the Dasycladaceae.

The recognition that *H. dinarica* was originally calcitic, not aragonitic, has important implications for diagenetic studies of the carbonates in which this microfossil occurs (e.g. the oil-bearing Shuaiba Formation of the Middle East). Because it was originally calcitic it would not have been leached during meteoric diagenesis, resulting in possible underestimations of the amount of meteoric diagenesis in previous studies.

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THE RELATIONSHIP OF THE MESOZOIC BIVALVE *ATRETA* TO THE DIMYIDAE

by P. HODGES

ABSTRACT. Material recently collected from the Lower Lias (Lower Jurassic) of South Wales shows evidence of dimyarian musculature in *Atreta intusstriata* (Emmrich) proving that the previous assignment of *Atreta* to the monomyarian Plicatulidae Watson, 1930, by Cox (1964) is incorrect. The genus is therefore reassigned to the Dimyidae Fischer, 1886. A lectotype and paralectotypes are designated from material located in the Emmrich collection at the Geiseltal Museum, Halle, Germany.

ETALLON (1862) erected *Atreta* and described the main diagnostic features, namely two projecting teeth, dimyarian musculature and anastomosing riblets in the right valve. Five species were listed as belonging to this genus: *Ostrea blandina* d'Orbigny, 1849, *Spondylus dichotomus* Buvignier, 1852, *Plicatula striatissima* Quenstedt, 1858, *Crania humbertina* Buvignier, 1852, and *Atreta imbricata* sp. nov. The last two were described, but none was figured and no type species selected. Rollier (1917) later invalidly selected *Atreta jurensis* Etallon, 1862, as type species.

The designation of *Ostrea blandina* as type species was made by Cox (1964), who considered Etallon's generic diagnosis extremely doubtful due to the generally poor preservation of the material available. He noted also that several authors after Etallon had failed to observe any musculature in species of this genus. Although he admitted that the main characteristics were allied to the Dimyidae, he nevertheless placed *Atreta* in the Plicatulidae due to his doubts about the presence of dimyarian musculature.

RELATIONSHIP OF THE DIMYIDAE TO OTHER BIVALVE FAMILIES

The Dimyidae comprises species which are suborbicular in outline, cemented by the right valve and with dimyarian musculature. Thiele (1935), Newell in Moore (1969) and Vokes (1980) placed the Dimyidae in the superfamily Pectinacea, which is otherwise made up entirely of monomyarian families. Newell's classification is as follows:

Order PTERIOIDA Newell, 1965

Suborder PTERIINA Newell, 1965

Superfamily PECTINACEA Rafinesque, 1815

Families PTERINOPECTINIDAE Newell, 1938; LEOPECTINIDAE Krasilova, 1959; AVICULOPECTINIDAE Meek and Hayden, 1864; DELTOPECTINIDAE Dickins, 1957; PSEUDOMONOTIDAE Newell, 1938; POSIDONIIDAE Frech, 1909; OXYTOMIDAE Ichikawa, 1958; ENTOLIIDAE Korobkov, 1960; PECTINIDAE Rafinesque, 1815; MONOTIDAE Fischer, 1887; BUCHIIDAE Cox, 1953; PLICATULIDAE Watson, 1930; SPONDYLIDAE Gray, 1826; TERQUEMIIDAE Cox, 1964; DIMYIDAE Fischer, 1886.

Nevesskaya *et al.* (1971) proposed a classification based on an analysis of shell structure and soft parts (gills and stomach) in extant bivalves. All are filter feeders, cemented or byssally attached. Their classification was:

Order PECTINOIDA Adams and Adams, 1857

Superfamily DIMYACEA Fischer, 1886

Family DIMYIDAE Fischer, 1886

Superfamily SPONDYLACEA Gray, 1826

Families TERQUEMIDAE Cox, 1964; PLICATULIDAE Watson, 1930; SPONDYLIDAE Gray, 1826.

Yonge (1975) noted major resemblances between the mantle, shell and viscero-pedal mass in extant species of the Dimyidae and Plicatulidae and proposed the following classification:

Superfamily PLICATULACEA Yonge, 1975

Families DIMYIDAE Fischer, 1886; PLICATULIDAE Watson, 1930.

Waller (1978) disagreed with Yonge's interpretation of the ligament in the Dimyidae and Plicatulidae and offered a new interpretation of primary ligament, shell structure and soft tissue in extant species of the Pteriomorphia. Utilizing cladistic analysis a revised classification was proposed, which is adopted here:

Order OSTREOIDA Férussac, 1822

Suborder OSTREINA Férussac, 1822

Superfamily DIMYACEA Fischer, 1886

Superfamily PLICATULACEA Watson, 1930

Superfamily OSTREACEA Rafinesque, 1815

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. NMW, National Museum of Wales, Cardiff; BMNH, British Museum (Natural History), London; BGS, British Geological Survey, Keyworth; BCM, Bristol City Museum, Bristol; GM, Geiseltal Museum, Halle, Germany.

Superfamily DIMYACEA Fischer, 1886

Family DIMYIDAE Fischer, 1886

Genus ATRETA Etallon, 1862

Synonyms. *Diploschiza* Conrad, 1866; *Cyclostreon* Eichwald, 1868; *Dimyopsis* Bittner, 1895; (*vide* Cox 1964).

Type species. *Ostrea blandina* d'Orbigny, 1849, p. 375, from the Oxfordian of France; subsequent designation of Cox 1964, p. 45.

Range. Early Rhaetian to Campanian of Europe and North America.

Diagnosis. Small, suborbicular, often slightly oblique; right valve attached by the greater part of its surface, internally shallowly concave, bordered by a raised ridge, inner shell layer generally missing exposing inner surface of outer shell layer with divaricating or anastomosing riblets ending in some species as transverse crenulations of the raised ridge; left valve almost flat with commarginal lamellose ornament, internal of valve showing suboval dimyarian musculature, resilium pit small, crura short and thin.

Atreta intusstriata (Emmrich, 1853)

Plate 1, figs 1–10

- + .1851 *cf. Ostrea placunoides* Munster; Schafhäütl, p. 413, pl. 7, fig. 7a–c.
- v*1853 *Ostrea intusstriata* Emmrich, p. 377.
- .1855 *Spondylus liasinus* Terquem, p. 327, pl. 23, fig. 7a–d.
- .1861 *Ostrea interstriata* Emmrich; Moore, p. 501, pl. 16, fig. 25.

- .1864 *Plicatula intus-striata* (Emmrich); Dumortier, p. 74, pl. 1, figs 13–16.
- .1865 *Plicatula liasina* (Terquem); Terquem and Piette, p. 107, pl. 13, figs 11–13.
- .1865 *Plicatula lotharingiae* Terquem and Piette, p. 109, pl. 13, figs 14 and 15.
- .1865 *Plicatula parkinsoni* Bronn; Terquem and Piette, p. 108, pl. 13, fig. 16.
- .1866 *Plicatula intusstriata* (Emmrich); Capellini, p. 484, pl. 6, fig. 12.
- .1867 *Plicatula intusstriata* (Emmrich); Stefano, p. 147, pl. 6, figs 35 and 36.
- .1876 *Plicatula liasina* (Terquem); Tate and Blake, p. 369.
- .1884 *Spondylus liassinus* (Terquem); Simpson, p. 178.
- .1884 *Spondylus intus-striatus* Tate; Simpson, p. 178.
- .1893 *Plicatula intusstriata* (Emmrich); Greco, p. 128.
- .1907 *Plicatula intusstriata* (Emmrich); Joly, p. 23.
- .1916 *Dimyopsis* (*Plicatula*) *intusstriata* (Emmrich); Goetel, p. 158.
- .1917 *Plicatula (Atreta) intusstriata* (Emmrich); Rollier, p. 536.
- .1917 *Plicatula (Atreta) lotharingiae* (Terquem and Piette); Rollier, p. 536.
- .1917 *Plicatula (Atreta) liasina* (Terquem); Rollier, p. 536.
- .1917 *Plicatula (Atreta) ambigua* Rollier, p. 537.
- .1929 *Plicatula (Dimyopsis) intusstriata* (Emmrich); Lanquine, p. 60.
- .1933 *Dimyodon intus-striatus* (Emmrich); Arkell, pl. 29, fig. 5.
- .1936 *Plicatula intusstriata* (Emmrich); Joly, p. 95.

Lectotype. Designated herein; GM MLU2/GM/HS.1, (plaster cast NMW 90.16G.2) attached right valve from the ‘Gervillienbildung’ (Rhaetian) of Kössen, Austria.

Dimensions. Height 11 mm, length 9 mm, anterior length 4 mm.

Paralectotypes. GM MLU1/GM/HS.1–10, (plaster cast NMW 90.16G.1) from the ‘Gervillenschichten’ (Rhaetian) of Sonntagshorn mountain, Bavaria, Germany; GM MLU3/GM/HS, (plaster cast NMW 90.16G.3) from the ‘Gervillienbildung’ (Rhaetian) of Eipelgraben bei Staudach, Bavaria, Germany; GM MLU2/GM/HS.2, details as lectotype.

Material. NMW 15.131.G9; NMW 20.349.G10; NMW 20.349.G16; NMW 20.362.G47; NMW 22.345.G384; NMW 22.345.G387–390; NMW 22.345.G392; NMW 22.345.G401–409; NMW 46.311.G12; NMW 65.345.GR26; NMW 67.121.G88; NMW 67.121.G138; NMW 83.22G.145–152; NMW 83.22G.174; NMW 83.22G.176–182; NMW 90.16G.1–3; BMNH L77133; BMNH L77176; BMNH L77194–L77195; BMNH L18104; BGS Zd14; BGS 312; BGS 91845–91863; BCM 9964 (9 specimens).

Stratigraphical range. Early Rhaetian – early Sinemurian (*resupinatum* Subzone)

Geographical range. United Kingdom (Moore 1861; Tate and Blake 1876; Simpson 1884; Arkell 1933; Hodges 1987), France (Terquem 1855; Dumortier 1864; Terquem and Piette 1865), Belgium (Joly 1907, 1936), Germany (Goetel 1916), Austria (Schafhäütl 1851), Italy (Capellini 1866; Stefano 1867; Greco 1893)

Description. Externally oyster-like, generally small, suborbicular to subovate in outline, often oblique, inequivalve, inequilateral, hinge line straight to slightly convex; right valve attached by most of its surface area, hinge area rarely preserved; left valve rather flattened often following the contours of the underlying attached valve, with external ornament of commarginal imbrications, valve margins closed.

Internally, right valve shallowly concave with raised ridge around the shell margin; inner shell layer missing exposing inner surface of outer shell layer with ornament of numerous divaricating anastomosing fine riblets, number increases with size, with up to four orders of bifurcation, originating at the umbo and terminating at the margin of the raised ridge, giving a crenulated appearance on the crest of the raised ridge. No hinge structures or muscle scars seen. Left valve has dimyarian musculature, anterior adductor muscle scar suboval in outline, posterior adductor slightly larger, suborbicular in outline and bilobed, muscle scars symmetrically positioned at about one third of the height below hinge line. Hinge structures not seen.

Remarks. Emmrich’s (1853, p. 376) description made no direct reference to any type material. He mentioned only that his species was widespread in the ‘Gervillienbildung’ (Rhaetian) of the Austrian Alps and was found at Partenkirchen, Kreuth and Sonntagshorn mountain. His main

collection housed at the Geiseltal Museum, Martin-Luther Universität, Wittenberg, Halle, Germany, contains three limestone blocks collected from Sonntagshorn, Kössen and a locality near Staudach (pers. comm. Dr G. Krumbiegel). One block (GM MLU1/GM/HS) has one syntype, a second (GM MLU2/GM/HS) two syntypes, and the last (GM MLU3/GM/HS) has ten specimens encrusted on '*Ostrea haidingeriana*' Emmrich.

Schafhäütl (1851) described and figured three right valves of this species from the Rhaetian of the southern Bavarian Alps, and compared them with the Muschelkalk species *Ostrea placunoides* Munster; he did not erect a name. His specimens were housed in the Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich but were destroyed during the Second World War. Emmrich (1853) made reference to Schafhäütl's description when describing material he collected from the Rhaetian of the Austrian Alps which he named *Ostrea intusstriata*. Although he produced no figure of his species, his description mentions quite clearly the anastomosing riblets on the inside of the attached right valve and their termination on the raised ridge at the shell margin. There can be little doubt, from the features he described and from his reference to Schafhäütl's description and figures, that his material is conspecific with specimens common in the Rhaetian and Lower Lias of Europe.

In Terquem's (1855) description of *Spondylus liasinus* mention is made of two cardinal teeth and muscle impressions below the beaks. A further mention of two cardinal teeth was made by Terquem and Piette (1865) when describing their *Plicatula lotharingiae*.

The shape of the muscle scars in this species and in particular the bilobed posterior adductor show a close resemblance to those seen in the extant species *Basiliomya goreauii* Bayer, 1971 and *Dimya corrugata* Hedley, 1902. Both these species belong to the Dimyidae; they were discussed in full by Yonge (1978). This provides further evidence of the close relationship between *Atreta intusstriata* and extant species of the Dimyidae.

Mode of life. It is presumed that *Atreta* was an epifaunal filter-feeder which lived permanently attached to the shells of other molluscs. It is found both in the marginal and off-shore facies of the Lower Jurassic. It has been observed encrusting the bivalves *Gryphaea arcuata*, *Pinna* (*Pinna*) *similis*, *Plagiostoma giganteum* and *Antiquilina succincta*. Large shells such as *Plagiostoma* can exhibit encrusted *Atreta* to a density of up to twenty per 0.01 sq. m. It is often found in association with other encrusting bivalves such as species of *Liostrrea*.

EXPLANATION OF PLATE I

Figs 1–10. *Atreta intusstriata* (Emmrich). 1, lectotype GM MLU2/GM/HS. 1, (plaster cast NMW 90.16G.2), internal of right valve; 'Gervillienbildung' (Rhaetian); Kössen, Austria. 2, paralectotype GM MLU2/GM/HS.2; details as in 1. 3, NMW 83.22G.182; internal of right valve attached to *Plagiostoma giganteum* Sowerby, showing anastomosing riblets; *bucklandi* Zone, Lower Lias; between Cwm Nash and Nash Point, South Glamorgan, South Wales. 4, paralectotype GM MLU1/GM/HS, (plaster cast NMW 90.16G.1); internal of right valve; 'Gervillienbildung' (Rhaetian); Sonntagshorn Mountain, Bavaria, Germany. 5, NMW 83.22G.182; external view of left valve attached in life position, details as in 3. 6, NMW 83.22G.178; internal of right valve attached to *Plagiostoma giganteum* Sowerby; *bucklandi* Zone, Lower Lias; 1.6 km E of Nash Point, South Glamorgan, South Wales. 7, paralectotypes GM MLU3/GM/HS.1–3, (plaster cast NMW 90.16G.3); internal of right valves attached to '*Ostrea haidingeriana*' Emmrich; 'Gervillienbildung' (Rhaetian); Eipelgraben bei Staudach, Bavaria, Germany. 8, paralectotypes GM MLU3/GM/HS.4–5; detail as in 7. 9, paralectotype GM MLU3/GM/HS.5; detail as in 7. 10a, NMW 83.22G.174; silicified left valve internal showing dimyarian musculature; *semicostatum* Zone, Lower Lias; temporary excavation 400 m N of Ford Motor Company site, Bridgend, Mid Glamorgan, South Wales. 10b, Detail as in 10a; dimyarian muscle scars highlighted for clarity, showing anterior adductor and bilobate posterior adductor. Magnifications: 1–8, $\times 2$; 9, $\times 3$; 10a, b, $\times 4$.

All specimens were coated with ammonium chloride prior to photographing, with the exception of figure 10.



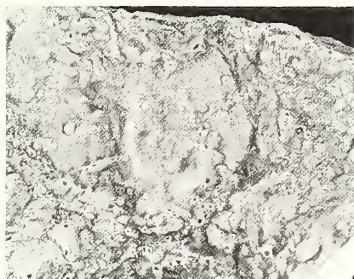
1



2



3



4



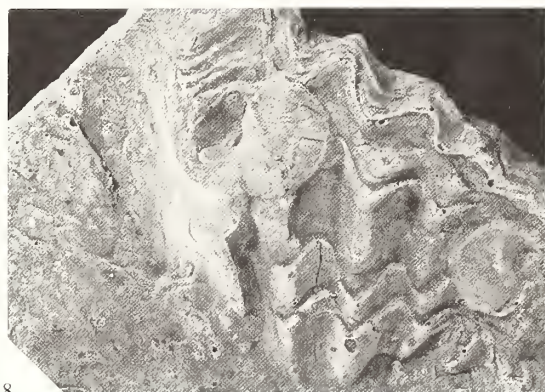
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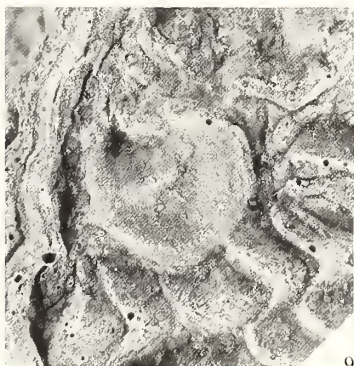
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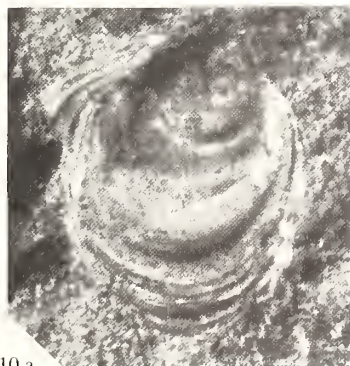
7



8



9



10 a



10 b

DISCUSSION

The evidence presented here of dimyarian musculature in *Atreta* confirms the observations of Etallon (1862). The assignment of this genus to the monomyarian Plicatulidae by Cox (1964) is therefore incorrect. *Atreta* is transferred to the Dimyidae based on the diagnostic characteristics described and also on the close similarity with musculature in modern species of this family. The stratigraphical range of the Dimyidae is thus extended back to the early Rhaetian.

Although an entire specimen with conjoined valves has been observed (NMW.83.22G.182), the left valve of members of this genus is rarely seen. Therefore they are known almost exclusively by the attached right valves, which due to preservation generally lack any evidence either of musculature or dentition, almost certainly a result of the loss of an aragonitic shell layer. This opinion has been given previously by Eudes-Deslongchamps (1860) and Cox (1964). Stenzel (1964) showed that the prodissoconch of the oyster *Crassostrea virginica* (Gmelin) is aragonitic, whereas the adults are mainly calcitic. This adds further credence to the possibility of shell layer loss in *Atreta*.

Atreta intusstriata (Emmrich) reached its highest population density in the Rhaetian of Europe where it was often used as a stratigraphical indicator. On the evidence of this species alone Lower Lias beds have been incorrectly designated as Rhaetian.

Acknowledgements. I thank the Ford Motor Company, Bridgend for permission to collect during excavations at their main factory site. Dr G. Krumbiegel kindly supplied plaster casts of syntypes in the Emmrich collection at the Geiseltal Museum, Halle. I thank Dr M. G. Bassett, Dr R. M. Owens and Mrs K. Bryant of the National Museum of Wales, Dr N. J. Morris and Mr R. Clevely of the British Museum (Natural History), Dr H. C. Ivimey-Cook of the British Geological Survey and Dr P. R. Crowther of the Bristol City Museum for access to material in the collections of their institutions.

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THE FIRST MESOZOIC PSEUDOSCORPION, FROM CRETACEOUS CANADIAN AMBER

by WOLFGANG SCHAWALLER

ABSTRACT. The first Mesozoic pseudoscorpion (Arachnida, Pseudoscorpionida) from Cretaceous (Campanian) amber collected in southern Alberta, Canada, is described. The specimen is a deutonymph and belongs to the family Chernetidae, but further taxonomic assignment is impossible. Some observations and deductions on its palaeobiology are made.

PSEUDOSCORPIONS (Arachnida, Pseudoscorpionida) are extremely rare as fossils, mainly because of their small size and the weak sclerotization of their cuticle. Nearly all fossil pseudoscorpions previously described came from Tertiary ambers of various ages and provenance, and all were assigned to modern families or even genera. Recently, three extremely well-preserved fossil fragments were described from Middle Devonian sediments near Gilboa, New York (Shear *et al.* 1989), belonging to a single species of a new family. In this enormous gap in the fossil record, between Eocene (45 Ma) and Middle Devonian (380 Ma), nothing is known about the evolution of this species-rich arachnid order (Chamberlin 1931; Beier 1932*a*, 1932*b*). Here the first record of a Mesozoic pseudoscorpion is reported. It is preserved in good condition and allows morphological documentation from several sides by a special technique (Schlee and Glöckner 1978). It is embedded in Cretaceous Canadian amber, dated as Campanian, 70–85 Ma (McAlpine and Martin 1969). The fossil belongs to the Recent family Chernetidae. A further taxonomic assignment is impossible mainly because the specimen is a deutonymph: the second of four post-hatching stadia in pseudoscorpions.

McAlpine and Martin (1969) gave a general account of the Canadian amber and mentioned several arthropod inclusions. Some spiders are under examination (Selden, personal communication). Another Cretaceous amber, the Lebanese amber (Aptian or Neocomian, 110–140 Ma), has aroused considerable interest (Schlee and Dietrich 1970). It contains a few spiders (unpublished material in the amber collection of the natural History Museum, Stuttgart, Germany) and also a pseudoscorpion: Whalley (1980), in a paper on neuropteran insects from Lebanese amber, incidentally mentioned a single pseudoscorpion among spiders and mites. Nothing is shown about its location, morphology or taxonomy.

GEOLOGICAL SETTING

The amber piece with the pseudoscorpion was collected by R. Mussieux, R. Solkoski and L. Strong, staff of the Provincial Museum of Alberta, at Grassy Lake, Southern Alberta, Canada, in 1976. Precise coordinates of the site are on file at the Royal Tyrrell Museum of Palaeontology and are available to qualified investigators on request. This locality was not listed by McAlpine and Martin (1969) among more than thirty localities in Canada and Alaska, where Cretaceous amber has been found. The primary amber deposits in Canada were dated as Campanian. When undisturbed, most Canadian amber lies along bedding planes in coal or carbonaceous sediments. However, most amber particles are found in secondary positions washed ashore in rivers and lakes.

MATERIAL AND METHODS

Preservation. The specimen is incomplete: the tibia and chela of the right pedipalp are lacking, the right pedipalp femur is somewhat damaged and the left pedipalp chela is broken in its basal part, the tips of the left tarsi I, II, IV are cut off, and the abdominal segments are wrinkled, particularly on the end of the abdomen.

From the wrinkled abdomen and because of some accompanying fungi mycelia it is concluded that the pseudoscorpion was embedded in the tree resin after death or that only the moulted cuticle was fossilized. Preservation is the same as in those amber fossils which have been heated artificially or naturally (Schlee, personal communication). Amber and its included fossils could have been heated in their primary or secondary fossil sites by different events.

Methods. The amber piece was embedded in polystyrol resin. After solidification, this amber-polystyrol-block was cut and polished under water to avoid heating. After morphological documentation under the microscope in a definitive plane, this technique was repeated for studying other views of the fossil.

DISCUSSION

Relationships

The fossil has two trichobothria laterally on the movable pedipalp finger and is therefore a deutonymph (assuming Recent conditions can be applied to the Cretaceous). A satisfactory classification of a juvenile pseudoscorpion is nearly impossible; furthermore, most of the Recent genera are fixed only by typological characters and not by synapomorphies. The fossil itself shows no unique character which would justify a new genus, so I avoid assigning this Cretaceous pseudoscorpion to a known or new genus or species.

The monotarsate legs, the structure of the chelicerae and the form of the carapace point without doubt to the Cheliferoidea (Atemnidae, Chernetidae, Cheliferidae, Withiidae). The Atemnidae can be excluded here, because all members of this family have a basally inserted tactile seta on tarsus IV (this seta is clearly absent in the fossil). Most of the Cheliferidae/Withiidae have eyes on the carapace and have distinctly more slender pedipalps than has the fossil; therefore the Cretaceous specimen is placed in the remaining Chernetidae. However, Recent chernetids usually have a poisonous tooth only on the movable pedipalp finger (the fossil has such a tooth also on the fixed finger). Accessory teeth on the pedipalp fingers are sometimes absent also in Recent deutonymphs of the Chernetidae, so perhaps adults of the Cretaceous species had such teeth.

The trichobothriotaxy of the pedipalp chela of the fossil seems incomplete: in Recent deutonymphs of the Chernetidae, the fixed finger has three trichobothria laterally (Mahnert 1982). But the insertion of the trichobothria is difficult to recognize in this amber specimen and, furthermore, some fungal mycelia are impeding visibility, so this irregularity should not be weighed too heavily.

Palaeobiology

Two further fossils are embedded in the same piece of amber (Text-fig. 1B), a mite and a juvenile insect larva or a collembolan. They are, together with the pseudoscorpion, members of the same Cretaceous biocoenosis, and not of a caenocoenosis as in other fossil sites apart from amber. These accompanying animal groups are typical inhabitants of Recent pseudoscorpion biotopes.

The fossil has a galea on its chelicera which proves that spinning behaviour existed in pseudoscorpions during the Cretaceous. So, the present deutonymph very probably spun a silken moulting chamber. Spinning activity of pseudoscorpions is already known from the Middle Devonian (Shear *et al.* 1989). Recent pseudoscorpions spin not only moulting chambers but also capsules for their eggs and for hibernation. The Cretaceous pseudoscorpion was able to groom itself



TEXT-FIG. 1. A, chernetid pseudoscorpion (deutonymph) from Cretaceous Canadian amber; body length (with chelicerae), 1.35 mm. B, mite (left) and juvenile insect larva or collembolan (right) from the same piece of amber as the pseudoscorpion; body length of the mite about 0.4 mm.

by the cheliceral serrulae. The animal, as a predator, used poison in grasping its prey, shown by the palpal venom teeth. The situation of the palpal trichobothria point to the same mode of orientation as in Recent species. The granulate cuticle (as in most of the Recent Chernetidae and Cheliferidae) may suggest a drier biotope; possibly this Cretaceous species lived in or under the bark of the tree which produced the amber.

SYSTEMATIC PALAEOLOGY

Order PSEUDOSCORPIONIDA Banks, 1895

Family CHERNETIDAE Chamberlin, 1931

chernetid gen. et sp. indet.

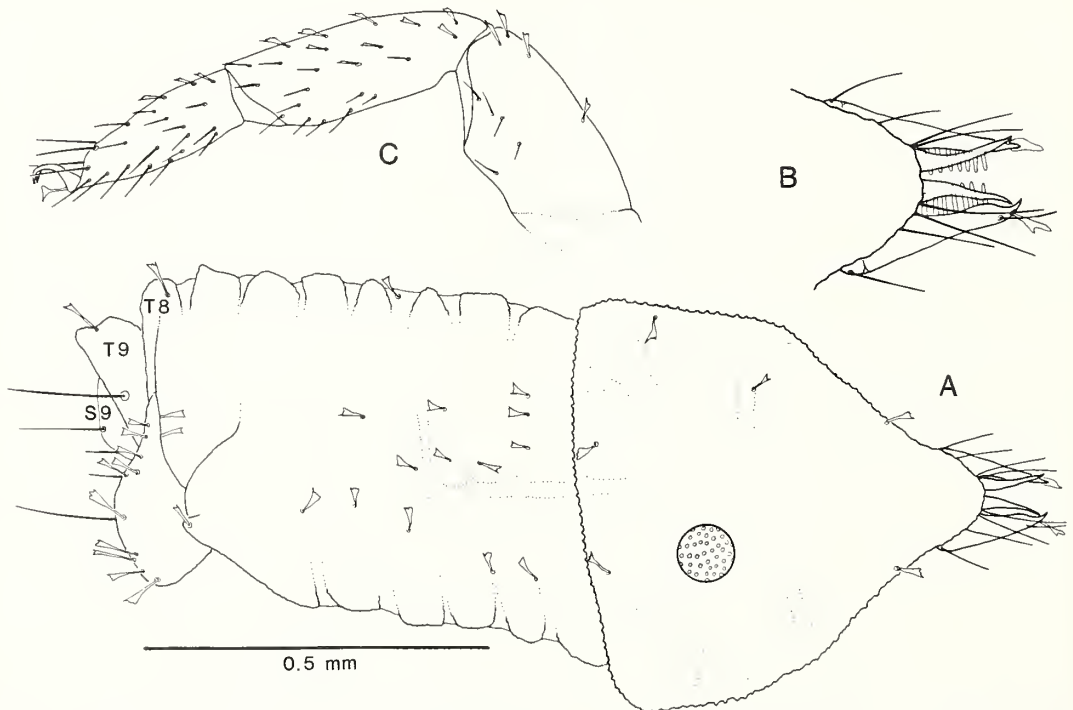
Text-figs 1-3

Material. A single specimen in Cretaceous Canadian amber from Grassy Lake, Alberta. Deposited in Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

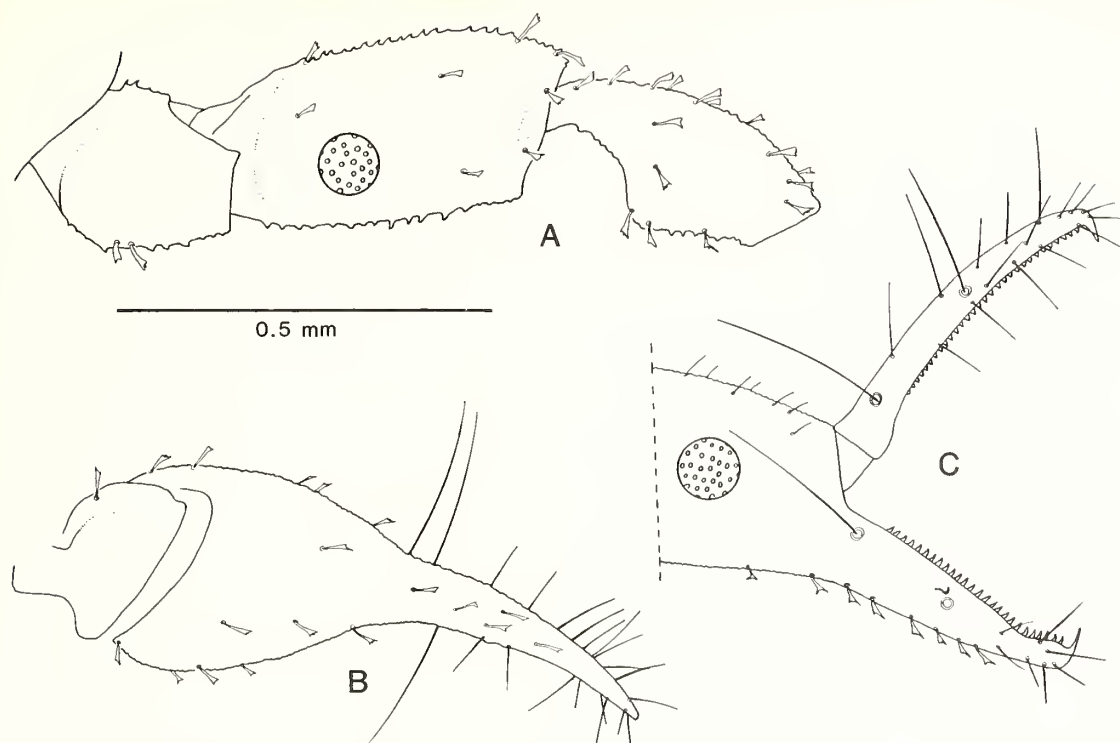
Description. Body length (with chelicerae) 1.35 mm. Cuticle of the body and of the appendages with granules. Carapace without eyes lenses and without eyes spots. Maximal width: 0.59 mm, median length: 0.58 mm. Carapace strongly narrowed in front, surface with two weak cross-furrows and basally with three short longitudinal furrows. Surface with uniform granulation and with irregularly inserted dentate bristles.

Abdomen with ten visible segments. At least the first tergites separated medially. Last tergite with two long tactile setae, tergites otherwise with dentate bristles (as on carapace). Number and position of all tergite bristles and details of the sternites not determinable.

Chelicerae have fixed and movable fingers without inner teeth. Movable finger with galea distally, its detailed



TEXT-FIG. 2. Chernetid pseudoscorpion (deutonymph) from Cretaceous Canadian amber. A, dorsal view of carapace and abdomen. B, chelicerae with galea, tactile setae and serrulae, $\times 1.66$ in relation to scale bar. C, leg IV.



TEXT-FIG. 3. Chernetid pseudoscorpion (deutonymph) from Cretaceous Canadian amber. A, left pedipalp trochanter, femur and tibia from dorsal view. B, left pedipalp chela from dorsal view. C, left pedipalp fingers from lateral view with teeth and recognizable trichobothriotaxy.

structure not visible. Basis of chelicera with at least four setae, their insertions covered by carapace. Movable finger with subgaleal seta distally. Serrula exterior with at least seven lamellae, structure of the serrula interior and of the flagellum not determinable.

Pedipalps: femur 0.49 mm long and 0.24 mm wide, tibia 0.38 mm and 0.19 mm, and chela 0.83 mm and 0.28 mm. Granulation on medial and lateral side of femur and tibia distinct, not so prominent on the chela and very faint towards the tip of the fingers. Surface with dentate bristles irregularly inserted, fingers with acute bristles distally. Trichobothriotaxy cannot be completely documented: movable finger with two trichobothria laterally (deutonymph), fixed finger with one trichobothrium laterally near basis and probably with a further trichobothrium in the middle; trichobothria on the medial side not visible. Fixed finger with twenty-six uniform and acute teeth, movable finger with thirty; both fingers with a distinct poisonous tooth; no accessory teeth.

All legs monotarsate. Tibia I 0.27 mm, tarsus I with claws 0.35 mm, tibia IV 0.43 mm, tarsus IV with claws 0.37 mm long. Tarsus I not modified; all claws simple, not dentate. Bristles on tibia and tarsus laterally dentate, medially acute; subterminal seta simple, acute; tibia and tarsus without tactile seta. Details of the coxae not visible without grinding away the legs.

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